PALEOBIOLOGY OF *ARCHAEOHIPPUS* (MAMMALIA; EQUIDAE), A THREE-TOED HORSE FROM THE OLIGOCENE-MIOCENE OF NORTH AMERICA

By

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by

Jay Alfred O’Sullivan

This study is dedicated to my wife, Kym. She provided all of the love, strength, patience, and encouragement I needed to get this started and to see it through to completion. She also provided me with the incentive to make this investment of time and energy in the pursuit of my dream to become a scientist and teacher. That incentive comes with a variety of names – Sylvan, Joanna, Quinn. This effort is dedicated to them also. Additionally, I would like to recognize the people who planted the first seeds of a dream that has come to fruition – my parents, Joseph and Joan. Support (emotional, and financial!) came to my rescue also from my other parents—Dot O'Sullivan, Jim Jaffe and Leslie Sewell, Bill and Lois Grigsby, and Jerry Sewell. To all of these people, this work is dedicated, with love.

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TABLE OF CONTENTS

page

ACKNOWLEDGMENTS iv

ABSTRACT viii

CHAPTERS

1 SMALL HORSE, BIG QUESTIONS 1

- Background 1
- Abbreviations and Conventions Used in This Study 8

2 A NEW SPECIES OF *ARCHAEOHIPPUS* (MAMMALIA; EQUIDAE) FROM THE ARIKAREEAN OF CENTRAL FLORIDA. 9

- Introduction 9
- Systematic Paleontology 11
- Discussion 24
- Conclusions 30

3 POPULATION DYNAMICS OF *ARCHAEOHIPPUS BLACKBERGI* (MAMMALIA; EQUIDAE) FROM THE MIOCENE THOMAS FARM FOSSIL SITE OF FLORIDA. 31

- Introduction 31
- Materials and Methods 33
  - First Reproduction in Modern Females 37
  - First Reproduction in Modern Males 39
- Results 40
- Discussion 44
  - Estimates of First Reproduction in Fossils 44
  - Age Dependent Mortality 46
  - Neonate Mortality Estimates 49
  - Estimates of Average and Potential Longevity 50
  - Paleoenvironmental Reconstruction of the Thomas Farm Fossil Site Based on Interpretations of Social Structure 51
  - Paleoenvironmental Reconstruction of the Thomas Farm Fossil Site Based on Interpretations of Dietary Preferences 52
- Conclusions 53

4 STABLE ISOTOPIC ANALYSIS OF EVOLUTIONARY HETEROCHRONY, BODY SIZE REDUCTION, AND DIETARY SPECIALIZATION IN *ARCHAEOHIPPUS BLACKBERGI* FROM THE MIOCENE THOMAS FARM FOSSIL SITE. 55

Introduction 55
    Heterochrony Affects Morphology, Life History, and Behavior 58
    Stable Isotopes in Tooth Enamel Archive Environmental and Behavioral Data ... 61
Materials and Methods 63
Results 65
Discussion 69
    Patterns of variation in $\delta^{18}O$ 69
    Evaluating Dietary Differentiation in *A. blackbergi* and *P. leonensis* 76
    Body Size and Resource Partitioning 76
    Patterns of variation in $\delta^{13}C$ 78
Conclusions 82

5 CLADISTIC ANALYSIS OF ANCHITHERE HORSES 86

Introduction 86
    Notes on Two Important Taxa 93
Materials and Methods 96
    Characters Used in this Analysis 98
    Taxa Used in this Analysis 102
Results 103
Discussion 112
Conclusions 119

6 SUPPOSITIONS AND CONCLUSIONS 121

Dwarfing and the Gulf Coastal Plain 122
Conclusions 127

APPENDIX - COMPARISONS OF KEY TAXA 131

    Observations on the Postcranial Skeleton 138
    Observations on Some Very Early Florida Equids 140
    Observations on Material at the AMNH 143
    Comments on Materials at USNM 148

LIST OF REFERENCES 149

BIOGRAPHICAL SKETCH 162

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
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PALEOBIOLOGY OF *ARCHAEOHIPPUS* (MAMMALIA; EQUIDAE), A THREE-TOED HORSE FROM THE OLIGOCENE-MIOCENE OF NORTH AMERICA

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May 2002

Chairman: Dr. Bruce J. MacFadden
Major Department: Zoology

The Oligocene-Miocene three-toed horse *Archaeohippus* (Mammalia; Equidae) is a brachydont browser that exhibits phyletic body size reduction and parahippine pedal adaptations. This study provides a summary of previous work regarding *Archaeohippus*, documents a new species of *Archaeohippus*, includes a life table analysis of *Archaeohippus blackbergi* from Thomas Farm, presents an analysis of stable isotopes from tooth enamel of three fossil horse taxa, and demonstrates phylogenetic relationships of *Archaeohippus* in a cladistic analysis.

Previous students of middle Cenozoic equids have been polarized in the phylogenetic placement of *Archaeohippus*. Some, emphasizing the importance of the primitive low-crowned teeth, have aligned this genus with the anchitheres *sensu stricto* such as *Anchitherium*. Those who focused on the shared derived condition of the manus and pes linked *Archaeohippus* with *Parahippus*. A new species from the middle Arikareean is the oldest and smallest known member of the genus. Its cheek teeth have relatively advanced characters such as crochets, additional enamel plications, and triangular hypostyles enclosing postfossettes, and its manus has reduced side digits and elongated medial phalanges; these characters link it with primitive parahippines.

The life table analysis of the population of *Archaeohippus blackbergi* from the early Hemingfordian Thomas Farm fossil site displays an age-dependent mortality spike in the young adult cohort that may be due to male combat, and which differs from the mortality profile of sympatric *Parahippus leonensis* and a population of *Miohippus obliquidens*, a close outgroup from the Oligocene of Wyoming. Analysis of stable isotopes of carbon from tooth enamel failed to elucidate dietary differentiation of the Thomas Farm equids. Oxygen isotopes revealed reduced ontogeny in *A. blackbergi* relative to *P. leonensis* but not *M. obliquidens*. A cladistic analysis of anchithere grade equids supported the monophyly of the genus *Archaeohippus* and placed it within the primitive parahippines.

This study provides insight into the paleobiology of *Archaeohippus*, the small browsing ecomorph of the first great equid adaptive radiation. This radiation produced a variety of equid forms in response to intensive global climate change that resulted in the fragmentation of forests and the appearance of extensive savanna ecosystems across North America.

CHAPTER 1
SMALL HORSE, BIG QUESTIONS

Background

Although the fossil remains are relatively fragmentary, the late Oligocene and early Miocene of Florida contain the equid genera *Miohippus*, *Archaeohippus*, *Anchitherium*, and *Parahippus*. In a broader phylogenetic context, these horses are important because they contain and define many of the character state transitions that occurred between advanced anchitheriine and primitive equine horses. Although much previous research regarding *Archaeohippus* has emphasized its uniqueness, the genus is equally interesting for those characters that suggest its affinities.

The affinities of *Archaeohippus* are obscured in part by a complicated taxonomic history. Specimens of this small, brachydont Miocene horse were first mentioned in publication by Cope (1886) from the early Barstovian Mascall Fauna of Oregon. Cope named the species *ultimus*, and assigned it to *Anchitherium*, a genus of large, tridactyl Miocene horses with brachydont teeth. Osborn (1910) placed both *Anchitherium* and *Archaeohippus* in the grossly paraphyletic subfamily "Anchitheriinae," what I will refer to as "Anchitheriinae" *sensu lato* (ASL). Osborn's (1910) formulation of this subfamily also included *Mesohippus*, *Miohippus*, *Parahippus*, and *Hypohippus*, as well as the European palaeothere *Anchilophus*. The inclusion of the palaeothere renders this concept of the subfamily polyphyletic. In a more recent look at Osborn's grouping (MacFadden 1992), ASL is defined as those horses with fully molarized P2-M3 that lack the dental characters that define the subfamily Equinae (Hulbert, 1989; Hulbert and MacFadden, 1991). This gradistic concept is MacFadden's (1992, 1998) paraphyletic "Anchitheriinae," derived from Osborn's (1910) definition and used by many museum collections today. Thus, ASL includes the late Eocene-Oligocene genus *Mesohippus*, its Oligocene-Miocene descendent *Miohippus*, and at least eight genera derived from one or more species of *Miohippus* (and perhaps *Mesohippus*). These taxa comprise the Arikareean anchithere radiation (AAR) of the New and Old Worlds, which begins in the late Oligocene (early Arikareean) and ends in the middle Miocene (late Clarendonian). The eight taxa in the AAR are *Archaeohippus*, *Desmatippus sensu* MacFadden (1998; *Anchippus sensu* Albright 1998, 1999), and *Parahippus*, as well as the "Anchitheriinae" *sensu stricto* (ASS) of MacFadden (1992): *Anchitherium*, *Kalobatipus*, *Sinohippus*, *Megahippus*, and *Hypohippus*. All members of the AAR are united by possession of a connection between the metaloph and the ectoloph (Evander, 1989). This connection is absent in *Mesohippus* and only occasionally present in *Miohippus* (both members of ASL). All members of ASS are united by "greatly increased tooth crown area and estimated body size, relatively well developed cingula, and loss of ribs between styles on cheek teeth" (MacFadden, 1992, p. 101), and a mesentocuneiform facet on MTIII (Osborn, 1918). Generally, they are further distinguished from other members of the AAR by the possession of robust, strongly divergent lateral digits on the manus and pes. Thus, these groups, arranged from most to least inclusive, are ASL>AAR>ASS. Of these, only ASS is possibly holophyletic.

Although the AAR remains poorly understood since the discovery of its major constituents over the past century, it has a sizeable fossil record. This record indicates an increase in morphological diversity unparalleled in the earlier evolutionary history of horses (Webb et al., 1995). Prior to the AAR, horse evolution in North America was much more conservative. Seminal work on the subject (Osborn, 1918; Matthew, 1924; Stirton, 1940) interprets this horse phylogeny as a series of gradistic genera, each genus distinguished from its ancestor by increased molar complexity and a slight increase in body size. This gradistic reconstruction of the evolutionary history of early horses may be due in part to very gradual evolution which produced only subtle morphological differences between different species. However, it may also reflect the bias of horse systematists. Much of the systematics of equids from the middle Miocene and younger is based on distinct characters in the complex occlusal surfaces of their molars, characters that are not always present in earlier equids. Another factor that explains the lack of resolution in the early part of the phylogeny of horses is the paucity of species-level cladistic studies on pre-Miocene taxa other than *Hyracotherium*. A recent revision of *Hyracotherium* (Froehlich, 1999) demonstrated that the traditional definition of this taxon includes a variety of primitive equids and other perissodactyls. Modern revisions of such taxa as *Epihippus*, *Orohippus*, *Mesohippus*, and *Miohippus* may similarly reveal more complex relationships than previously envisioned. Even considering this possibility, overall known equid morphological diversity was relatively low until the AAR was fully underway in the late Arikareean.

Certain lineages in the AAR demonstrate early phases of the trends in limb and tooth evolution that characterize the later radiation of advanced equids in the middle Miocene. The adaptive radiation of equine horses during the middle Miocene of North America is a well-studied macroevolutionary phenomenon that resulted in at least 11 late

Miocene clades (Webb and Hulbert, 1986; MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991; Hulbert, 1993a; for a review, see MacFadden, 1992). Morphological trends characteristic of this radiation include reduction of the side toes, elongation of distal limb elements, and increase in tooth crown height and occlusal complexity. These trends have been interpreted as adaptations to life in open country and a diet that included grasses (Marsh, 1879; Simpson, 1951; Janis, 1976; Janis et al., 1994; Behrensmeyer et al., 1992). These evolutionary trends can be traced back to the AAR in members of the genus *Parahippus*. Primitive members of this genus, sometimes assigned to the genus *Anchippus* (*sensu* Albright, 1998) or *Desmatippus* (*sensu* MacFadden, 1998), are dentally little more derived than advanced species of *Miohippus*. The most derived species of *Parahippus*, such as the Hemingfordian *P. leonensis*, possessed cheek teeth that were incipiently hypsodont and usually covered with cement. Its feet were tridactyl, but the lateral digits were reduced in length and thickness and held close to the middle digit, such that it was probably functionally monodactyl under normal locomotor conditions (Sondaar, 1968). These and other derived characters led Hulbert and MacFadden (1991) to identify *P. leonensis* as the nearest sistergroup of the middle Miocene adaptive radiation of equines.

The clade of large-bodied horses designated Anchitheriinae *sensu stricto* (ASS) is characterized by a suite of morphological trends that differ fundamentally from those that led to the advanced grazing horses (MacFadden, 1992 Fig. 5.15, node 3). These include an increase in body size without an increase in relative crown height or occlusal complexity of the molars (MacFadden, 1992), and perhaps an even more functionally tridactyl foot than that seen in many species of *Miohippus*. The lateral metapodials and phalanges are very robustly built and the lateral metapodials are not firmly appressed to the medial metapodial (Sondaar, 1968). Whereas the morphology of *P. leonensis* suggests that it may have been an early inhabitant of the first North American savannas (Hulbert and MacFadden, 1991), the morphology of members of the ASS (brachydont teeth and splayed digits) reflects a continuation of the forest-dwelling ecology of earlier equids (Sondaar, 1968).

Archaeohippus is perhaps the most enigmatic genus in the AAR and shows an interesting mosaic of primitive and derived features. Among anchitheres, it possesses a unique facial morphology, including a long pre-orbital region of the skull with a deeply pocketed malar fossa confluent with a deep lacrimal fossa. It possessed primitively brachydont teeth, but with slightly more occlusal complexity than that seen in the ASS. However, its pedal adaptations are as advanced as those of *Parahippus* (Matthew, 1932; Sondaar, 1968), with strongly reduced side metapodials appressed to the medial metapodial. In addition, *Archaeohippus* has been cited as an example of phyletic dwarfism (MacFadden, 1987; 1998). At approximately 20 kg (Janis et al., 1994), the estimated body weight of *Archaeohippus* is about half that of most species of *Miohippus*, the common equid of the late Oligocene. Dwarfing lineages that contradict Cope's Rule (Stanley, 1979) have been demonstrated in the fossil record of mollusks (Jablonski, 1997) and equids (MacFadden, 1987; Hulbert, 1993b). Some may be the result of directional selection for early maturation and reproduction (O'Sullivan, 2000). The ecology of *Archaeohippus* must have bridged that of the more ecologically distinct members of the AAR. Its primitively brachydont teeth indicate a diet of browse, like that of

Anchitherium, whereas its limb morphology suggests an affinity for open country, like *Parahippus*.

As stated above, in the original description of the type species *Archaeohippus ultimus*, Cope (1886) assigned material from Cottonwood Creek, Oregon, to the genus *Anchitherium*. In his description of fossils from the same locality from the Mascall Fauna of Oregon, Gidley (1906) erected a new genus, *Archaeohippus*, to distinguish this small brachydont horse from the anchitheres *sensu stricto*. The next named species, the somewhat larger and younger *Archaeohippus mourningi* (Merriam, 1913), was originally assigned to *Parahippus*. *Archaeohippus penultimus* was described from the Sheep Creek of Nebraska by Matthew (1924). Hay (1924) described both *Miohippus blackbergi* and *Parahippus minutalis* from the Garvin Gully Local Fauna of Texas. Simpson (1932) described *A. nanus* from the Thomas Farm Local Fauna of Florida.

Matthew (1932) recognized the derived nature of the pes and manus shared by *Archaeohippus* and *Parahippus* and the facial fossa shared by *Archaeohippus* and *Parahippus pristinus*, and suggested that *Archaeohippus* was a subgenus of *Parahippus*. In an excellent synthesis, Bode (1933) rediagnosed the species *Archaeohippus ultimus*, *Archaeohippus penultimus*, and *Archaeohippus mourningi*, and defended the generic status of *Archaeohippus*. Schlaikjer (1935, 1937) considered *Archaeohippus blackbergi* (=*Archaeohippus minutalis*) to be a dwarf *Parahippus*, as did White (1942). White's (1942) justification was that individuals in the Thomas Farm population of *A. blackbergi* variably possess advanced dental characters such as a crochet, additional plications, and a hypostyle that connects to the ectoloph and metaloph to close the postfossette. White (1942, p. 19) noted that the patterns of variation of the dentitions of other species of

Archaeohippus do not display these advanced characters, but are "simple and stable." Bode (1933) and Downs (1956) also noted that these characters were rare and weak when present in populations of *A. mourningi*, *A. penultimus*, and *A. ultimus*. Rather than accept the possibility that reduced variation in later species might involve the loss of advanced characters, Schlaikjer (1935, 1937) and White (1942) decided that the other species of *Archaeohippus* were convergent with *A. blackbergi*. White (1942) considered "*Parahippus*" *blackbergi* to be an intermediate between *Miohippus* and more advanced *Parahippus*. White (1942) also identified several teeth from Thomas Farm lacking a metaloph connected to the ectoloph as belonging to *Miohippus*. However, this character is variable within individual dentitions and can not be considered diagnostic when found in isolated teeth (Forsten, 1975).

Downs (1956) compared *A. blackbergi* with the western species and returned *A. blackbergi* to *Archaeohippus*. For the next two decades the debate was dropped, to resurface briefly in the work of Forsten (1975), who agreed with Downs (1956) that *A. blackbergi* is the correct name for the species of tiny horse found in both Texas and Florida during the Hemingfordian. More recently, Storer and Bryant (1993) identified *A. stenolophus* (Lambe, 1905) from the early Hemingfordian of Saskatchewan.

Including the new species, *Archaeohippus* includes five valid species that range from the middle Arikareean to the late Barstovian, a span of approximately 10 Ma. The geographic range of this genus extends across most of North America. In addition to Florida, Texas, Nebraska, South Dakota, Oregon, and California, specimens of *Archaeohippus* have also been found in Delaware (Emry and Eshelman, 1998) and Panama (Whitmore and Stewart, 1965). As noted in Osborn (1918, p. 96) the type of

Archaeohippus (?=*Parahippus*) *minimus* (Douglas, 1899) CM 713 from the early Barstovian of Montana seems to be a chimera composed of teeth from two taxa. The P3-M1 can be assigned to *Archaeohippus ultimus* based on size, morphology, age, and geographic location. A molar and a premolar that were included with the type are from a larger, more derived equid. *Archaeohippus stenolophus* (Storer and Bryant, 1993) from the early Hemingfordian of Saskatchewan does not belong within this genus as defined in this study.

Abbreviations and Conventions Used in This Study

AC = Amherst Collection; AMNH = American Museum of Natural History; ASL = "Anchitheriinae" *sensu lato*; ASS = Anchitheriinae *sensu stricto*; ap = anteroposterior; C = upper canine; c = lower canine; AAR = Arikareean Anchithere Radiation; CM = Carnegie Museum; I = upper incisor; i = lower incisor; L = left; L.F. = Local Fauna; M = upper molar; m = lower molar; Ma = Mega anna (millions of years ago), MCIII = metacarpal III; ml = mediolateral; MTIII = metatarsal III; NMC = National Museun of Canada; P= upper premolar; p = lower premolar; PU = Princeton University, now part of Yale Peabody Museum; R = right; UF = Florida Museum of Natural History, University of Florida

CHAPTER 2
A NEW SPECIES OF *ARCHAEOHIPPUS* (MAMMALIA; EQUIDAE) FROM THE ARIKAREEAN OF CENTRAL FLORIDA

Introduction

Late Oligocene and early Miocene fossils in Florida provide the best information of early Neogene terrestrial vertebrate faunas in eastern North America. These faunas include several taxa of Equidae. For example, at Thomas Farm, a rich Hemingfordian site in Gilchrist County, three equids are found: *Parahippus leonensis*, *Archaeohippus blackbergi*, and *Anchitherium clarencei* (Simpson, 1930, 1932; Bader, 1956; Forsten, 1975; MacFadden, 2001). In more recent years, tantalizing evidence of even older terrestrial faunas in Florida has been found. Those that include equids are the White Springs Local Fauna (Morgan, 1989), Cow House Slough (Morgan, 1989), Buda Local Fauna (Frailey, 1979), Brooksville Local Fauna (Patton, 1967), Brooksville 2 Local Fauna (Hayes, 2000), SB 1A Local Fauna (Frailey, 1978), and the Whitneyan I-75 Local Fauna (Patton, 1969). Albright (1998) reviewed all of these faunas and their biogeographic implications. To these is added a new site, Curlew Creek of Pinellas County, Florida (Fig. 1).

The purpose of this study is to describe the Curlew Creek equid (Figs. 2-4) as a new species of *Archaeohippus*. A partial skeleton (UF 160784) from this locality was recently acquired by the Department of Vertebrate Paleontology of the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville. The collector, Christian

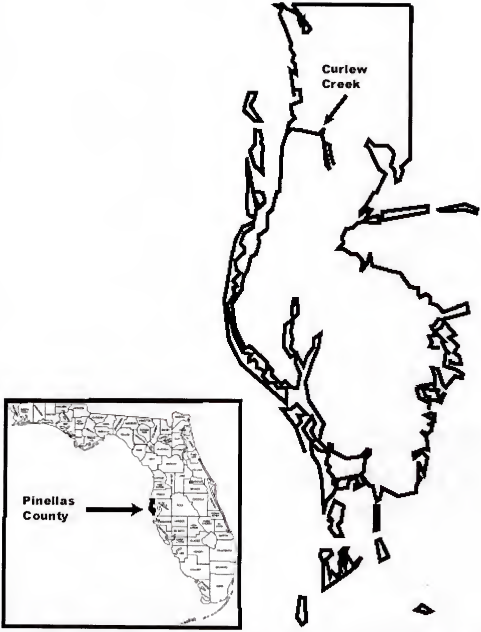


FIGURE 1. Map of the Curlew Creek locality (UF locality PI016) in Pinellas County, Florida. Insert map indicates the location of Pinellas County in the state of Florida.

B. Skillman, recovered this skeleton from a compacted clay layer that appears to be a paleosol, overlain by Quaternary alluvium and underlain by the Hawthorne Fm. (Webb, pers. comm.). The Tampa Bay Fossil Club acquired the specimen from the collector and donated it to the FLMNH. S. D. Webb and F. G. Hayes of the FLMNH visited the site and took field notes and samples. This specimen, found articulated *in situ*, represents the most nearly complete specimen of Arikareean *Archaeohippus* known.

Considering that this new taxon is based on a single specimen, intraspecific variation for pertinent characters can not be determined. However, interspecific comparisons were made with specimens of similar age grade and degree of wear. Referred specimens of the new species were recovered from a spoil pile that resulted from the excavation of a drainage ditch that empties into the creek ca. 1 km east of the type locality. Also present is a distal metapodial (UF 182407) with the well-developed keel and small size characteristic of the small peccary *Cynorca*. *Cynorca* in Florida is known from the late early Arikareean (Ar2 of Tedford et al., 1987) Cow House Slough site (Morgan, 1989; Albright, 1998: table 1) and the late early to early late Arikareean (Ar2-Ar3) Buda Local Fauna (Frailey, 1979; Hulbert, 1992, 2001).

Systematic Paleontology

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1821

Genus *ARCHAEOHIPPUS* Gidley, 1906

Type species. *Archaeohippus ultimus* (Cope, 1886).

Included species. *Archaeohippus ultimus* (Cope, 1886) from the early Barstovian of Montana (Douglas, 1903) and Oregon (Downs, 1956); *Archaeohippus mourningi* (Merriam, 1913) from the late Barstovian of California (Bode 1933); *Archaeohippus blackbergi* (Hay, 1924) from the early Hemingfordian of Florida (White 1942) and Texas (Forsten, 1975), and possibly Nebraska (Cook, 1965), South Dakota (Harkson and McDonald, 1967), and Delaware (Emry and Eshelman, 1998); *Archaeohippus penultimus*

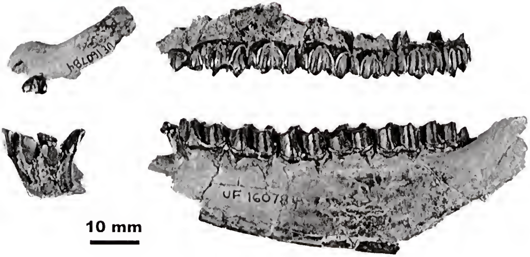


FIGURE 2. Dentition of UF 160784, holotype of *Archaeohippus mannulus*, sp. nov., lateral view of L premaxilla with I3, maxilla with dP1-M3, mandibular symphysis with i1-c, and mandible with dp1-m3 mandibular symphysis with right and left i1-c1.

(Matthew, 1924) from the late Hemingfordian of Nebraska; *Archaeohippus mannulus* sp. nov.

Revised generic diagnosis. Small equid (M1 AP length 10 - 14.5 mm); most species similar in size to *Mesohippus* and smaller than most species of *Miohippus*; facial region long; prominent dorsal preorbital and malar fossae with defined upper, lower, and posterior rims and deeply pocketed posteriorly (malar fossa present in *P. pristinus*, not present in *Anchitherium*, *Kalibatippus Hypohippus*); anterior edge of orbit over posterior M2 or anterior M3 (distinct from *Mesohippus* and most *Miohippus*); placement of internal posterior edge of zygomatic process of the maxilla well behind M3 (as in *Miohippus* and distinct from *Mesohippus*); narial notch dorsal to DP1.

Upper dentition. Elongated P2 with anterostyle; shape of upper molars nearly square (*Miohippus* usually rhomboidal); cement absent within fossettes with a thin layer

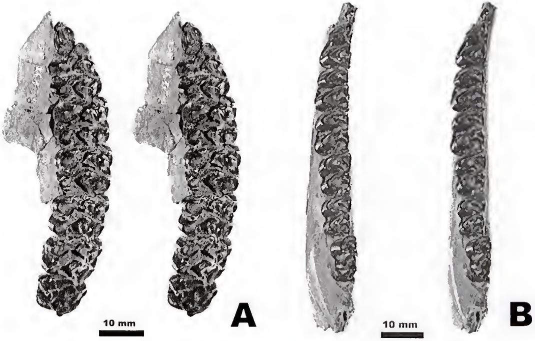


FIGURE 3. Stereo occlusal views of left **A**, upper and **B**, lower cheek teeth of UF 160784, holotype of *Archaeohippus mannulus*, sp. nov. Note additional ridges originating on the metaloph and extending into the medivallum on P2-P3; triangular hypostyles enclosing postfossettes; constricted connection of the paraconule to the protocone; strong ribs on the ectoloph; well-developed metastyle; and small crochets present on P3-M2. Also note the large hypoconulids on p2-m2 and strong m3 heel.

sometimes present on ectoloph; M3/m3 reduced with posterior half of M3 noticeably ML narrower than anterior half; crochet and additional plications variably present in individuals of smaller, older species, and generally absent in younger species; medivallum (see Fig. 5) between protoloph and metaloph closed by crochet (as in *Merychippus*) infrequently; styles distinct; strong metastyle as in *Parahippus* (weak in *Mesohippus*, *Miohippus*); prominent ribs between styles on ectoloph unlike *Anchitherium*, which has weak ribs when present; metaloph connected to ectoloph (unlike *Mesohippus* and most *Miohippus*, but as in *Parahippus*), although individual teeth in a toothrow (especially M3) or deciduous premolars may have a weak or no connection;

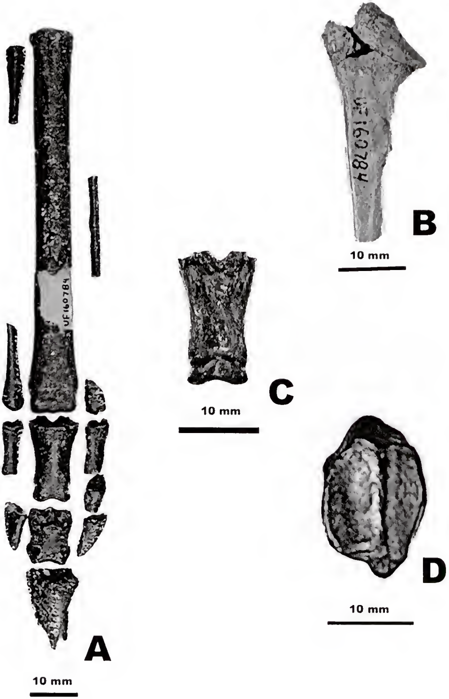


FIGURE 4. Postcranial elements of UF 160784, holotype of *Archaeohippus mannulus*, sp. nov. **A**, right manus; right proximal ulna; **B**, right patella with distal process; **C**, lateral view of proximal phalanx of the third digit displays the sharp ridges on the posterior edge of the articulation with MC 3, possibly a very cranially placed cruciate scar; **D**, articular surface of patella with lower apical process.

hypostyle usually triangular with a tiny fossette (Type 3 of Clark et al., 1967) and strong lingual ridge (the actual hypostyle according to White's [1942] terminology), and usually closes postfossette (postfossette open in *Miohippus equinanus*); protoconule distinct from protocone; and metaconule usually distinct from hypocone in unworn cheek teeth and deciduous premolars.

Lower dentition. Metalophid high and confluent with metastylid in early to medium wear in contrast to *Mesohippus* and many *Miohippus* species; metaconid-metastylid twinning usually present in p3-m3, although only for about 2 mm on unworn teeth, twinning present also on dp2, but not on p2; m3 heel present, sometimes with small basin or fossettid, although heel and basin not as large as in *Miohippus*; outlines of protolophid and hypoconid angular, more V-shaped than that of *Anchitherium clarencei* and *Parahippus leonensis*; lingual cingulum in permanent lower cheek teeth usually present, unlike *M. obliquidens* and *P. leonensis*.

Postcranial skeleton. Manus and pes with second and fourth metapodials reduced midshaft and extensively attached to third metapodial as in *Parahippus*; distinct MC III volar tubercle for attachment of the tendon for the muscle interossei; MC III and MT III elongate, slender, and round-oval in cross-section (as opposed to flattened cross-sections of *Mesohippus*, *Miohippus*, and *Anchitherium*); no facet on MT III for mesentocuneiform (this facet seen in *Anchitherium*, *Kalibatippus*, *Hypohippus*, not in *Parahippus)*; proximal phalanx of pes has short but prominent V-scar formed by the confluence of scars for oblique sesamoid ligaments; cuboid facet on MT III as in *Miohippus*; proximal phalanx of the third digit more elongate than in *Miohippus*, *Mesohippus*, and *Anchitherium*, with a midshaft "waist" not seen in these taxa, which usually have wide, flat phalanges.

ARCHAEOHIPPUS MANNULUS, sp. nov.

Holotype. UF 160784, a partial skull consisting of the R and L maxillae with all cheek teeth, L premaxilla with I3 and associated C, and a cranium endocast; partial L mandible with dp1-m3, mandibular symphysis with R and L I1-C; partial atlas and axis; partial distal humerus; R proximal radius; partial R and L distal radii; R proximal ulna; R scaphoid; R and L lunar; R cuneiform; R and L pisiform; R and L unciform; proximal sesamoid; R and L MC III; R and L proximal MC IV; R(?) distal MC II and MC IV; R and L proximal phalanges; R(?) medial phalanx; R and L distal phalanges; R patella.

Referred specimens. Isolated elements recovered from a spoil pile created by a creek-deepening project ca. 1 km east of the type locality include two complete (UF 182401, UF 182404) and two partial upper deciduous premolars (UF 182402, UF 182407), two partial upper cheek teeth (UF 182403, UF 182405), and three lateral phalanges: one proximal (UF 182408), one medial (UF 182409), and one distal (UF 182410).

Type locality. Curlew Creek, Pinellas County, Florida. Dunedin USGS 7.5' Quadrangle, sec. 14, T. 28S., R. 15E. UF locality PI016; detailed locality information on file.

Stratigraphic occurrence and age of the type locality. The holotype was collected from a compacted clay layer that is stratigraphically between Quaternary alluvium and the Hawthorne Group (Webb, pers. comm.). The age is late early–early late Arikareean (*sensu* Tedford et al., 1987) based on the presence of *Cynorca*.

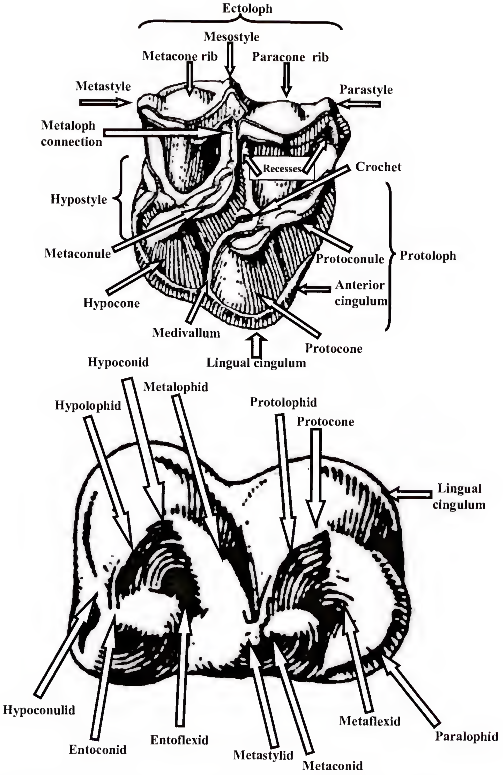


FIGURE 5. Drawing of UCMP 35894, P4 (top) and UCMP 35763, p4 (bottom) of *Parahippus* cf. *nebrascensis*, after Stirton (1941), illustrating structures discussed in the text.

Etymology. *mannus* is Latin for small horse (of Gaul); *mannulus* is the diminutive form; therefore, a very small horse or pony. Also, this name is a pun on the fact that the holotype of *A. mannulus* (UF 160784) is largely represented by a pair of hands (*manus*). Finally, inasmuch as its pronunciation echoes *A. nanus,* this species name is a tribute to the excellent name (an unfortunate victim of synonymization) erected by G.G. Simpson in 1932.

Diagnosis. Smallest species of *Archaeohippus* (M1-M3 length of 30 mm is at the lower end of the range of *A. blackbergi)*; P2-P3 have a ridge that originates on the metaloph and terminates lingually in the medivallum between the protocone and hypocone (Fig. 3A) (in *A. blackbergi* these ridges are submerged into the expanded hypocone, but a remnant is sometimes visible); cheek teeth have well-developed crochets and plications on the postfossette as in *A. blackbergi* (but not later species); metastyle is stronger than in *Miohippus*, but smaller than in most individuals of later species; hypoconulid relatively large, plate-like, and usually enclosed on all sides by enamel (prior to extreme wear); all postcranial skeletal measurements smaller than any other known species of *Archaeohippus*. The distal humerus has a high, narrow capitulum as in *A. blackbergi*, that terminates posteriorly in a ridge sharper than that of *A. blackbergi.*

Description. The holotype, UF 160784, is a young adult male with m3 hypoconid just coming into wear.

The lower incisors (Fig. 3B) form a semicircular arcade with a diameter of 20 mm (this measurement is approximate due to distortion of position of the I3s). The centers of the labial surface of the i1s have two low, narrow ridges that form a shallow groove between them. These ridges do not extend as far as the crowns of the incisors, which show moderate wear. The i2s possess small (~2mm) grooves with raised rims; these grooves are oblique to the long axis of the tooth surface and are just medial to the center line. All lower incisors have infundibula; the I3in the L premaxilla is narrower with a deeper infundibulum than the i3s.

The lower canines (see Fig. 2) are robust and project ~6 mm beyond the occlusal level of the incisors, identifying the specimen as a male. Each canine has a thin ridge on the anterior surface and a weaker ridge on the posterior surface. The labial surface has a slight rib and a weak cingulum linking the ridges. The upper canine is smaller, has weaker ridges and a stronger rib and cingulum.

The upper cheektooth series (Figs. 2, 3A; Table 1) includes a large, double-rooted DP1. It has an anterior cusp and a posterior basin. The DP1 is tilted relative to the other upper cheek teeth. The anterior crista of the cusp tilts dorsally and is thus removed from occlusion with the dp1. The posterior crista and the basin are rotated ventrally, which puts them in strong occlusion with the p2.

The protoloph is not connected to the ectoloph on both P2s, the L P3, and the R M3. The remaining upper cheek teeth possess thin, but complete, connections. The P2 paracone is strongly ribbed. The anterostyle and parastyle are both distinct. Both the P2 and P3 possess an additional ridge or cuspule in the medivallum between the protocone and hypocone. This ridge attaches to the metaloph just above the hypocone. The hypostyle is triangular and encloses the posterior of the postfossette in all but the L M3. As with the hypocone, all of the cones and conules are narrow and distinct. The connection between the protoconule and the protocone is constricted. Paracone and metacone ribs are clearly defined on the labial surface of the ectoloph. The metastyle is

Table 1. Comparison of measurements of the left upper cheek teeth of UF 160784, the holotype of *Archaeohippus mannulus*, with a sample of *Archaeohippus blackbergi* from Thomas Farm, with comments on the placement of UF 160784 relative to the sample from Thomas Farm.

Measurement	*A. mannulus*	*A. blackbergi* N, *x*, *s*, range	Comments
DP1 APL	7.5	12, 9.4,0.6, 8.2-10.4	below observed range
DP1 AMLW	4.27	12, 4.8, 0.3, 4.3-5.3	below mean
DP1 PMLW	5.04	12, 5.1, 0.3, 4.4-5.6	below mean
P2 APL	12.57	19, 12.9, 0.7, 11.6-14.8	below mean
P2 AMLW	10.27	19, 10.5, 0.5, 9.3-11.4	below mean
P2 PMLW	11.22	19, 11.2, 0.8, 9.0-12.4	equal to mean
P3 APL	10.92	15, 11.7, 0.5, 10.7-12.4	below mean
P3 AMLW	11.84	15, 12.8, 0.8, 11.3-13.5	below mean
P3 PMLW	11.74	15, 12.5, 0.9, 10.8-13.5	below mean
P4 APL	11.2	16, 11.7, 0.7, 10.3-13.01	below mean
P4 AMLW	12.79	16, 13.7, 0.7, 12.4-14.9	below mean
P4 PMLW	11.96	16, 13.0, 0.8, 11.1-14.1	below mean
M1 APL	10.46	15, 11.3, 0.6, 10.1-12.5	below mean
M1 AMLW	12.61	15, 13.4, 0.7, 12.1-13.9	below mean
M1 PMLW	11.98	15, 13.0, 0.8, 11.6-14.2	below mean
M2 APL	10.53	13, 10.9, 0.7, 9.8-12.4	below mean
M2 AMLW	12.46	13, 13.1, 0.9, 11.7-15.0	below mean
M2 PMLW	11.36	13, 12.4, 1.0, 11.0-14.3	below mean
M3 APL	8.85	23, 9.2, 0.5, 8.3-10.1	below mean
M3 AMLW	10.67	23, 11.0, 0.8, 9.1-12.5	below mean
M3 PMLW	9.24	23, 8.8, 0.9, 7.1-10.3	above mean

distinct but subequal in height to the mesostyle. Crochets are present on P3-M2; they do not close off the prefossette except in late wear. Additional plications are infrequent and small.

In the mandibular dentition (Figs. 2, 3B; Table 2), the dp1 is small. It is completely unworn, as it would not occlude with the DP1 until late wear. The p2 - m3 all possess strong labial cingula and weak lingual cingula. Only the p2 has a complete lingual cingulum. Hypoconulids on p2 - m2 are large, plate-like, and fully enclosed by enamel. The m3 heel is large; there is a completely enclosed fossettid between the heel and entoconid. At this stage of wear, the m3 metalophid contacts, but is distinct from, the metastylid. Although too worn to display metaconid-metastylid twinning, faint grooves in the enamel of p3-m3 suggests that slight twinning may have been present in unworn teeth.

Table 2. Comparison of measurements of the left lower cheek teeth of UF 160784, the holotype of *Archaeohippus mannulus*, with a sample of *Archaeohippus blackbergi* from Thomas Farm, with comments on the placement of UF 160784 relative to the sample from Thomas Farm.

Measurement	*A. mannulus*	*A. blackbergi* N, *x*, *s*, range	Comments
p2 APL	11.6	11.2, 0.5, 10.2-12.1, 35	above mean
p2 AMLW	5.5	5.5, 0.4, 5.0-6.9, 35	equal to mean
p2 PMLW	7.2	6.7, 0.3, 6.1-7.5, 35	above mean
p3 APL	9.9	10.6, 0.5, 9.6-11.4, 26	below mean
p3 AMLW	6.9	7.3, 0.4, 6.7-8.3, 26	below mean
p3 PMLW	8.2	7.9, 0.5, 6.9-9.0, 26	above mean
p4 APL	10.0	10.8, 0.5, 9.9-11.8, 30	below mean
p4 AMLW	7.5	8.1, 0.3, 7.4-8.7, 30	below mean
p4 PMLW	8.4	8.3, 0.5, 7.2-9.1, 30	above mean
m1 APL	10.0	10.5, 0.6, 9.2-11.4, 41	below mean
m1 AMLW	8.0	7.7, 0.4, 7.1-8.5, 41	above mean
m1 PMLW	7.1	7.2, 0.5, 6.3-8.2, 41	below mean
m2 APL	10.1	10.4, 0.6, 9.2-11.8, 36	below mean
m2 AMLW	7.5	7.3, 0.4, 6.6-8.0, 36	above mean
m2 PMLW	6.7	6.6, 0.5, 5.5-7.7, 36	above mean
m3 APL	10.6	11.2, 0.7, 9.9-12.4, 30	below mean
m3 AMLW	6.3	6.3, 0.4, 5.8-7.2, 30	equal to mean
m3 PMLW	5.3	5.3, 0.5, 4.7-6.6, 30	equal to mean

The elements of the R elbow joint are present. The partial distal humerus has a high, narrow capitulum (AP width = 12 mm) that terminates posteriorly in a sharp ridge. The ulna (Fig. 4B) has a proximal humeroulnar notch width of 5.8 mm and a distal humeroulnar notch width of 10.9 mm. The radioulnar notch is a flat facet that provides a loose fit with the fossa on the posterior surface of the proximal radius. The partial proximal radius (articular ML width, 16.8 mm; articular AP width, 9.4 mm) has a shallower fossa than that typically seen in *A. blackbergi*.

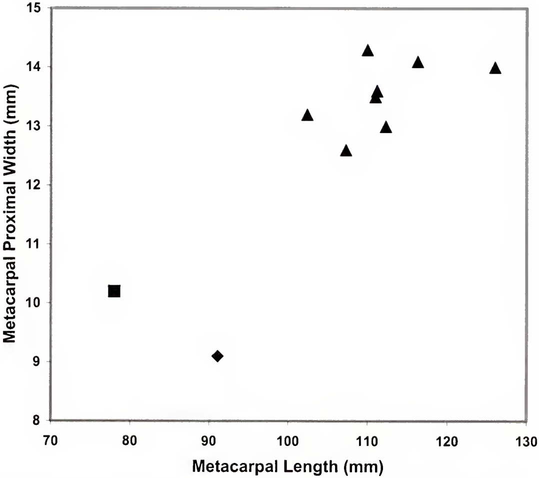


FIGURE 6. Bivariate comparison of metacarpal measurements for UF 160784 (■), the holotype of *Archaeohippus mannulus*, sp. nov., with those for a sample of *A. blackbergi* from Thomas Farm (▲). Metacarpal length for UF 160784 is 69.7% that of the sample mean for Thomas Farm *A. blackbergi*. Also included is *Mesohippus* metacarpal UF 201941 (◆).

The metacarpals are ~78% as long as the shortest *A. blackbergi* metacarpal from Thomas Farm (Fig. 6). The R MC III is 78.3 mm long, with proximal width of 9.3 mm and distal articular width of 9.1 mm (maximum distal width, 10.2 mm). The MC III is round-oval in cross-section. The scars for the attachment of the interosseus metacarpal ligaments extend to the epicondyles. The groove between these scars on the volar surface of MC III is distinct but shallow. Proximal articular facets resemble those of *A. blackbergi* (as figured by Sondaar, 1968: fig. 11.2) except that, of the two facets for articulation with the unciform (hamatum), the anterior facet is less concave and the posterior facet more cranially directed. The anterior and posterior facets for articulation with the MC IV are large. The volar tubercle for attachment of the tendon for the muscle interossei is distinct. The shaft broadens slightly distally. The sagittal keel of the distal articular surface is strongly developed posteriorly, weaker distally, and not present anteriorly. The lateral metacarpals are broken, so lengths can not be measured. However, from their impressions on the MC III, it is clear that they were nearly as long as the MC III. The midshaft sections that are preserved are very thin in the ML plane, approximately 1.5 mm. The proximal and distal articular surfaces are relatively large and well developed.

The length of the proximal phalanx of the third digit (16.8 mm) is <77% that of the smallest of 101 measured proximal phalanges of Thomas Farm *A. blackbergi* (see Fig. 7). Its length is 5.7 standard deviations from the mean of the Thomas Farm sample. The proximal phalanx of the third manual digit (length, 16.8 mm; proximal width, 9.7 mm; distal width, 7.3 mm; Fig. 4C) displays distinct oblique, central, lateral volar, and sublimis scars. The posterior edge of the articulation with MC III has two sharp ridges, possibly an extension of the cruciate scar. The groove that articulates with the keel of the distal MC III is broad and shallow posteriorly and becomes less distinct near the anterior lip of the articular surface. The medial phalanx of the third digit (length, 11.7 mm; proximal width, 9.2 mm; distal width; 9.2 mm) has a proximal articular surface (ML width, 7.9 mm; AP length; 5.4) that abuts a posterior sesamoid articular area that is relatively large. The distal condyles are broad, with pointed projections at the lateral extremes. The articular surface of the condyles covers in excess of 180 degrees of the distal surface. The proximal articulation of the distal phalanx (length, 18.3 mm) is nearly perpendicular to the plantar surface.

Of the posterior limb, only the R patella is present. It (Fig. 4D) is noteworthy in that its downward apex has a pointed process.

Discussion

The holotype of *A. mannulus* demonstrates that this species' estimated body size range was below that of *A. blackbergi*, while the referred lateral phalanges (UF 182408, UF 182409, and UF 182410) overlap the lower end of the size range seen in *A. blackbergi* from Thomas Farm. Therefore, the largest known *A. mannulus* were about the size of the smallest *A. blackbergi*. Estimates of the body mass of *A. mannulus* vary widely. The following mass estimates are the central estimates only, without confidence intervals. M1 length yields estimates of approximately 40 kg using MacFadden's (1986) equid regression and 20 kg using Damuth's (1990) nonselenodont ungulate regression. Scott's (1990) regressions based on equid postcranials yield 4.3 kg and 11 kg for two proximal radius measurements; and 10 kg, 23 kg, and 25 kg for three measurements of the third metacarpal. The barking deer *Muntiacus muntjak* is an extant animal whose stature (head-body length = 90-100 cm; shoulder height 45-65 cm [Boitani and Bartoli, 1982]) is similar to that of *A. blackbergi* from Thomas Farm. *M. muntjak* weighs 14-16 kg; the slightly larger four-horned antelope *Tetracerus quadricornis* weighs 17-21 kg (Boitani and Bartoli, 1982). Based on these modern analogues, a reasonable mass estimate for *A. blackbergi* is a range of 15-20 kg. This would place the smaller *A. mannulus* in the range of 10-15 kg (and possibly lower), like the banded duiker *Cephalophus zebra* (Boitani and Bartoli, 1982).

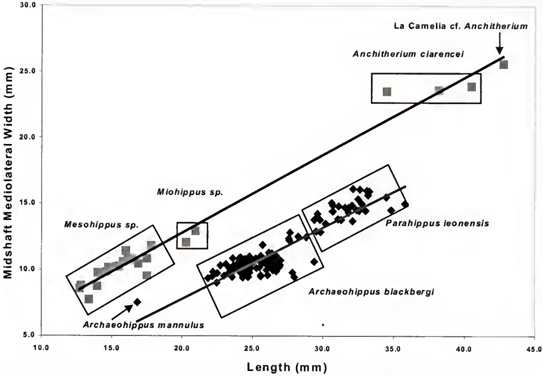


FIGURE 7. Bivariate comparison of measurements of the proximal phalanx of the third digit for a sample of *Archaeohippus blackbergi* (N=101) from the Hemingfordian Thomas Farm fossil site of Florida, *Parahippus leonensis* (N=33) from Thomas Farm, *Mesohippus* sp. (N=17) from Oligocene sites in Nebraska, Wyoming, and Florida, *Miohippus* sp. (N=2) from Nebraska and Florida, *Anchitherium clarencei* (N=3) from Thomas Farm, cf. *Anchitherium* (N=1) from the Barstovian La Camelia Mine of Florida, and the holotype of *Archaeohippus mannulus* from the Curlew Creek fossil site of Florida.

In many ways, UF 160784 looks like a miniature version of *A. blackbergi*. Its metacarpals and phalanges have similar proportions. However, tendon and ligament scars are less distinct in the holotype of *A. mannulus* than in *A. blackbergi*. This is not surprising in such a small animal with absolutely smaller functional demands placed on its skeleton.

It is instructive to compare postcranial measurements of the type of *A. mannulus* with those of *Mesohippus bairdi* (Prothero and Shubin, 1989: table 10.4). While the length of the MC III (78.3 mm) falls within the range of *Mesohippus bairdi* (78 - 85 mm, n = 3), it is much more slender (ML width, 9 mm) than that of *M. bairdi* (ML width, 13 -

14 mm; n = 2). The mediolateral width of the proximal radius of the type of *A. mannulus* is 16.8 mm. In *M. bairdi*, this measurement is 23 - 26 mm (n = 3). Thus, while *A. mannulus* was similar in size to *M. bairdi*, one of the smallest species of *Mesohippus*, it was far more gracile. *A. blackbergi* obtained overall postcranial proportions roughly equivalent to those of the larger species, *Mesohippus barbouri*, which also possessed similarly elongate distal limb elements. The Barstovian species *A. mourningi* is larger still.

Another trend in the evolution of this genus is an apparent reversal in cheektooth complexity. Crochet and additional plications are variably present in *A. mannulus* and *A. blackbergi*, and lost in later species. This contrasts with the trend in parahippines. The crochet and additional plications are variably present in primitive species of *Parahippus*, and are more consistent and better developed in advanced species such as *P. leonensis*. Therefore, experimentation in molar cusp morphology occurred in the lineages of *Archaeohippus* and *Parahippus* for some time after these taxa diverged. In *Archaeohippus*, this experimentation did not persist much beyond the Hemingfordian. Of the samples studied by Downs (1956), the Barstovian species *A. ultimus* has minute crochets in only 20% of the sample and in *A. mourningi* the crochet was entirely absent. Individual plications on the metaloph are common but minute in *A. ultimus*, and exceedingly rare in *A. mourningi* (Downs, 1956). In *Parahippus,* dental elaboration continued on into the lineage that resulted in the merychippines (Hulbert and MacFadden, 1991). In this lineage, elaboration of occlusal complexity accompanies an increase in crown height and the consistent presence of cementum to form a suite of cheektooth adaptations for grazing.

The presence of a well-developed crochet and midshaft reduction of the side digits in the early Arikareean specimen UF 160784 implies that these characters were not independently acquired in *Archaeohippus blackbergi* and in the lineage that leads to *Parahippus leonensis*, but are derived from a common ancestor. Even without having had the opportunity to see *A. blackbergi* with its little crochet, W. D. Matthew (1924) saw enough derived characters shared by *Archaeohippus* and *Parahippus* to place the former as a subgenus of the latter. While there is no doubt that these taxa are generically distinct, as defended by Bode (1933) and subsequent authors, future efforts may reveal that they are, in fact, sister taxa.

Archaeohippus mannulus, *A. blackbergi*, and *P. leonensis* share derived features of the upper dentition including straight-sided protoloph and metaloph, and primary cones that are narrow and columnar. The width of the cones does not change significantly between middle and late wear; thus, the base of the protocone does not share an extensive contact with the base of the paracone. This latter condition is also in part due to the crescentic protoconule which occupies most of the area directly lingual to the paracone. The ectoloph has the curved profile common in many *Miohippus* and later equids. Beneath this curved ectoloph form small recesses on either side of the narrow, columnar paracone and metacone. This is also seen in one of the equid upper molars from I-75 (UF 208904) and *Anchippus texanus* from Toledo Bend, Texas (Albright, 1999). In *P. leonensis*, these recesses are filled with cementum. Low, conical cones without adjacent recesses beneath the ectoloph are present in *Mesohippus*, *Anchitherium*, *Miohippus equinanus*, *M. obliquidens*, *Parahippus pristinus*, the Cowhouse Slough equid, and, to some degree, the equids from Brooksville. The broad contact between the protocone and paracone may explain the weak development of the crochet when present in these taxa – there is not enough space at the base of the metaloph for this structure to expand.

In the lower cheek teeth, the outstanding feature of *A. mannulus* is the large, flat hypoconulid completely enclosed by enamel. In Thomas Farm *A. blackbergi* dentitions at a similar stage of wear, the hypoconulid is either ML narrow and peg-like (less than half as wide as the tooth), or it is very flat and without enamel on its posterior surface.

A comparison of relevant postcranial characters in *A. mannulus* and Thomas Farm *A. blackbergi* and *P. leonensis* follows. The volar tubercle for attachment of the tendon for the muscle interossei is distinct but not large as in *A. blackbergi*; instead it resembles the condition found in *P. leonensis*. The scarring for the attachment of the interosseus metacarpal ligaments is not as distinct as in *A. blackbergi*, although the scars do extend to the epicondyles. The groove between these scars on the volar surface of MC III is distinct, but not as deep as in *A. blackbergi*. Proximal articular facets resemble those of *A. blackbergi* except that, of the two facets for articulation with the unciform (hamatum), the anterior facet is less concave and the posterior is more vertically directed. The shaft broadens distally as in *Parahippus leonensis*. In *A. blackbergi*, the shaft has a more uniform width from midshaft to the distal end, with only a slight broadening proximal to the epicondyles, making the epicondyles very distinct. As in *A. blackbergi*, the sagittal keel of the distal articular surface is strongly developed distally and posteriorly but not anteriorly. The proximal and distal articular surfaces of the lateral metacarpals are relatively large and well developed as in *A. blackbergi*. Although I mention distinctions between the metacarpal morphologies of these three taxa, their shared, derived character states outweigh their differences.

A. mannulus, *A. blackbergi*, and *P. leonensis* share derived metapodial characters including: relative elongation, round/oval cross-section (as opposed to flat/oval) with a groove between scars for interdigital ligaments, and reduction of the epicondyles. In these ways they differ from *Mesohippus*, *Miohippus* (including *M. equinanus*), *Anchitherium*, and the equid from Cowhouse Slough. Additional distinction from some *Mesohippus* and the Cowhouse Slough equid is lack of the pronounced distal projection of the keel found in these taxa.

The proximal phalanx of the third pedal digit of *A. blackbergi* typically has strong scars from the attachment of ligaments, while the homologous phalanx in the manus has weaker and fewer scars. The proximal phalanx of the third manual digit from the holotype of *A. mannulus* has distinct oblique, central, lateral volar, and sublimis scars, and thus resembles a pedal phalanx of *A. blackbergi*. The degree of development of the short V-scar resembles that of *A. blackbergi* and *P. leonensis*, with enlarged, converging oblique scars distinct from the central scar. This differs from *Anchitherium clarencei*, which does not have large oblique scars. The V-scar has been interpreted as an indicator of increased stability (reduced lateral mobility) at the joint in the lineage of equine horses (Sondaar, 1968). The posterior edge of the articulation with MC III has two sharp ridges, possibly a very vertically placed cruciate scar occasionally seen in *A. blackbergi*. This development would also serve to reduce lateral mobility at the metacarpal-phalanx III joint. The groove that articulates with the distal MC III keel resembles that seen in many *A. blackbergi* in that it is broad and shallow posteriorly and becomes less distinct near the anterior lip of the articular surface. The medial phalanx of the third digit resembles that of *A. blackbergi*. The proximal articular surface abuts a posterior sesamoid articular area that is relatively larger than that of most *A. blackbergi* from Thomas Farm.

The proximal ends of the lateral metacarpals generally conform to the pattern seen in *A. blackbergi* (for the similarly constructed *Parahippus*, see Sondaar, 1968: fig. 13) except that the neck just distal to the articular facets is relatively thinner and smoother in *A. mannulus*, and the MC II facet for articulation with the trapezoideum is more rounded.

The pointed process on the downward apex of the patella of *A. mannulus* is not seen in those of *A. blackbergi* from Thomas Farm; though relatively smaller, it is found in some *P. leonensis*.

Conclusions

Archaeohippus is one of the most widely distributed early Miocene equids in North America. The oldest quarry samples of this taxon come from the early Hemingfordian of the Gulf Coastal Plain. Taxa that have been proposed as Arikareean age sister taxa include *Parahippus pristinus* (Matthew, 1932), *Miohippus equinanus* (Skinner et al., 1968), and the equid from the Cowhouse Slough local fauna (Webb et al., 1995). In the absence of a cladistic analysis of these taxa, none can be completely eliminated from consideration. However, the holotype of *A. mannulus* represents the first unambiguous evidence of *Archaeohippus* from the Arikareean. Thus, the implication found in Webb et al. (1995) that *Archaeohippus* had its beginning in Florida, then spread throughout North America in the Hemingfordian, may indeed be accurate.

CHAPTER 3

POPULATION DYNAMICS OF *ARCHAEOHIPPUS BLACKBERGI* (MAMMALIA; EQUIDAE) FROM THE MIOCENE THOMAS FARM FOSSIL SITE OF FLORIDA

Introduction

The Miocene horse genus *Archaeohippus* (Gidley, 1906) may be an example of phyletic dwarfism. Phyletic dwarfism, in its broadest sense, is size decrease in ancestral-descendant lineages, and is a form of paedomorphosis. It is the result either of the process called neoteny, where somatic growth is retarded and sexual maturity is not; or of progenesis, where somatic growth rate is unchanged but sexual maturation rate is accelerated, causing an early onset of sexual maturity. Attainment of sexual maturity is strongly correlated with a dramatic decrease in somatic growth rate (Alberch, et al., 1979).

Body size has a strong influence on mammalian physiology, life history variables, and ecology (McNab, 1980; Eisenberg, 1981). Thus, a single heterochronic dwarfing event can affect each of these (McKinney and Gittleman, 1995). The ecological benefits of size reduction in *Archaeohippus* should include reduction of competition for resources with other ungulate species. In particular, small herbivores are capable only of processing small amounts of food, and so are dependent on high quality herbage (Janis, 1976). However, they are well-suited to survive in environments with a dry season during which resources are available only in small patches, and are thus good indicators of such environments (Ravosa et al., 1995).

Age of reproductive maturity and gestation length are correlated with body size (Eisenberg, 1981). Compared with artiodactyls, perissodactyls have large neonates and long gestations (Millar, 1981). Size reduction through dwarfing might have provided *Archaeohippus* with a way to reduce life history parameters such as gestation length and age of first reproduction relative to larger, plesiomorphic equids.

The Thomas Farm fossil site of Gilchrist County, Florida, is the largest early Miocene (ca. 18 million years) terrestrial site east of the Mississippi River (Simpson, 1932, Pratt, 1990). Site taphonomy indicates that the formation of the fossiliferous deposit occurred over a period of at most thousands of years (Pratt, 1990). Thomas Farm contains one of the earliest and largest known samples of *Archaeohippus*. Although a wide array of vertebrate taxa has been identified from Thomas Farm, the vast majority of large mammal fossils recovered belong to three-toed horses. The most common taxon is *Parahippus leonensis*, the incipiently hypsodont sister taxon of the younger grazing merychippine clade (Hulbert and MacFadden, 1991). The largest and rarest is the browser *Anchitherium clarencei* (MacFadden, 2001). The smallest horse taxon is *Archaeohippus blackbergi*.

The brief period of fossil accumulation provides an almost instantaneous sampling of the fauna. The Thomas Farm fossil site formed as a sediment cone within a sinkhole; thus it is not as taphonomically biased as a stream deposit (Pratt, 1990). Therefore, taxa can be treated as relatively intact populations in life table analyses of demographics. Hulbert (1984) performed such a study using mandibles of *P. leonensis* from Thomas Farm. He determined that the mortality profile indicated not a catastrophic accumulation of individuals, but an attritional assemblage that accumulated over many years.

The study presented here is an analysis of the population structure of *Archaeohippus blackbergi* from Thomas Farm with a comparison to *P. leonensis* from Thomas Farm (Hulbert, 1984) and other equid populations. Exploring the population dynamics of this taxon is part of a larger study of heterochrony and the evolution of *Archaeohippus*. This study has also provided insight into the workings of the dynamic life table as applied to fossil samples.

Materials and Methods

A life table analysis of a fossil population uses the proportions of individuals in each age class to estimate population characteristics such as age-related mortality, average longevity, and fecundity. Such an analysis (Table 3) was performed on the population of *Archaeohippus blackbergi* from Thomas Farm (Table 4). *Miohippus obliquidens* (Table 5), a taxon from the Orellan Harvard Fossil Reserve in Goshen County, Wyoming, was included in the analysis to reflect the plesiomorphic condition of a larger equid modeled to be close to the ancestry of *A. blackbergi*. At present, however, the identity of the nearest plesiomorphic sister taxon of *Archaeohippus* is unclear. In addition, comparisons will be made with Hulbert's (1984) study of the population of *Parahippus leonensis* (Table 5) from Thomas Farm.

Nine age classes are recognized for *Archaeohippus* jaws that correspond to age classes used by Hulbert (1984) on *Parahippus leonensis* from Thomas Farm. Classes one through five are based on patterns of tooth eruption, while classes six through nine are based on tooth wear criteria. Crown height measurements were taken at the metaconid. I will note how these classes differ for *A. blackbergi* vs. other taxa to which they have been applied.

Table 3. Life table for *Archaeohippus blackbergi* from the early Miocene Thomas Farm fossil site in Gilchrist County, Florida. N(x) is the number of mandibles and dp2s or p2s from the original sample that belong to a Class. D(x) is N(x) adjusted to fit a hypothetical population of 1000, and it can be obtained with the following formula: dx=[N(x)/N*1000]. L(x) of Class 1 is set at 1000, but for subsequent classes l(x+1)=l(x)-d(x). M(x) is fecundity, and it has been estimated as described in the text. For Class x, reproductive output =l(x)*m(x). Age-specific mortality q(x)=d(x)/l(x). Average longevity for a class is e(x)=(0.5duration(x)*d(x) + 1.5duration(x)*d(x)+1 + 2.5duration(x)*d(x)+2 ...until the oldest cohort in the population)/l(x).

Class	N(x)	d(x)	l(x)	m(x)	l(x)m(x)	q(x)	e(x)
1	0	0	1000	0.00	0	0.00	2.70
2	4	69	1000	0.00	0	0.07	2.10
3	6	103	931	0.00	0	0.11	1.63
4	11	190	828	0.10	86	0.23	1.20
5	22	379	638	0.29	185	0.59	0.87
6	5	86	259	0.41	105	0.33	1.10
7	3	52	172	0.41	70	0.30	0.90
8	4	69	121	0.41	49	0.57	0.56
9	3	52	52	0.41	21	1.00	0.30
Totals	58			2.02	516		

Unworn heights were rarely available because occlusion and wear coincide with full eruption. Not all of Hulbert's (1984) wear-based age class criteria derived from that author's study of *P. leonensis* are applicable to the *A. blackbergi* sample. For example, the linguaflexid is not as strongly developed in *A. blackbergi* as in *P. leonensis*; thus the linguaflexid does not persist through as many classes in *A. blackbergi*. *M. obliquidens* typically loses the p2 metaflexid after half the crown height is worn down.

Wear in *M. obliquidens* occurs earlier on p2-m1. Permanent premolars display more wear than m2 throughout the life of the dentition, and this is very obvious by Class 5. This wear pattern suggests that the permanent premolars erupt before m2 comes into occlusion. Seen also in other *Miohippus* species observed by this author, this wear

Table 4. Number of jaws and second deciduous and permanent premolars of *Archaeohippus blackbergi* from Thomas Farm in each age class, and the proportion of the sample of either category these represent. Second premolars were placed in age classes based primarily on wear criteria. In both categories, a sudden increase occurs in Class 5. This class is signaled by the occlusion of the m3, which is interpreted to correlate with the attainment of sexual maturity.

Class	Mandibles (N)	%	p2s (N)	%
1	0	0	0	0
2	2	6	2	8
3	4	12	2	8
4	4	12	7	28
5	11	33	11	44
6	4	12	1	4
7	2	6	1	4
8	3	9	1	4
9	3	9	0	0
Total	33		25	

pattern is not characteristic of *A. blackbergi* or *P. leonensis*, which clearly erupt m2 before erupting p2-p4.

The later wear classes in *A. blackbergi* are different than in *P. leonensis*. This is due to the low crown height of *A. blackbergi* teeth. For example, the last wear stage of *P. leonensis* has all lingual reentrant angles worn away on all but m3 (Hulbert, 1984: fig. 3). These features are present in the enamel of *A. blackbergi* down to the root of the tooth. Such complete loss of occlusal detail on all teeth would be much rarer in *A. blackbergi* than in the higher crowned dentition of *P. leonensis*, which does not possess detailed features near the roots.

Wear Classes (eruption based classes with *Equus* analogues in parentheses): Class 1- dp2-dp4 erupted, no m1 eruption; Class 2- m1 erupting or erupted, no m2; Class 3- m2 erupting or erupted, no m3; Class 4- p2-p4 erupting or erupted, m3 partially erupted (in *Equus*, the eruptions of p2 and p3 erupt during Class 3 at 2.5 years, while p4 erupts during Class 4 at 3.5 years, coincident with the start of m3 eruption); Class 5- m3 fully erupted, some wear; Class 6- m3 fully wearing except heel (may have slight wear on enamel, no exposed dentine in *A. blackbergi*); Class 7- m3 heel worn, m1 metaflexid is tiny (*M. obliquidens* m2 metalophid fully attached to metastylid); Class 8- m3 heel heavily worn (*M. obliquidens* m3 metalophid attached to metastylid); Class 9- all teeth heavily worn. In *P. leonensis*, p3 and p4 (and probably p2) erupt at the same time and *A. blackbergi* erupts p2-p4 nearly simultaneously, not sequentially as in *Equus* (Hulbert, 1984).

Table 5. Number of jaws of *Miohippus obliquidens* from the Harvard Fossil Reserve and *Parahippus leonensis* from Thomas Farm (from Hulbert, 1984) in each age class, and the proportion of the sample these represent. The *M. obliquidens* distribution differs from that of *A. blackbergi* in a) the greater representation of Class 1 individuals; b) the lesser representation of juvenile Classes 2-3; and c) the less distinct mortality spike in early adulthood, which extends through Classes 4-6. The *P. leonensis* distribution differs from that of *A. blackbergi* in a) the greater representation of Class 1 individuals; b) the very different mortality profile which lacks a spike at Classes 4 and 5, but instead increases gradually through Class 8.

	Miohippus obliquidens		*Parahippus leonensis*	
Class	Mandibles (n)	%	Mandibles (n)	%
1	3	13	3	4
2	1	4	5	7
3	1	4	9	12
4	4	16	8	11
5	6	24	6	8
6	4	16	12	16
7	3	12	14	19
8	2	8	14	19
9	2	8	3	4
Total	25		74	

From a sample of mandibles (MNI=33) and 25 deciduous and permanent lower second premolars, a dynamic life table was constructed for *Archaeohippus*. Convention requires an adjusted population of 1000 (Deevey, 1947), and this was achieved by multiplying all original numbers by 17.24. Age at which adulthood is attained in fossil horse populations can be calculated by comparing estimated rates of tooth wear with eruption of the third molar, an ontogenetic event strongly correlated with attainment of sexual maturity in modern horses and other ungulates (Sisson, 1927).

Wear rates are estimated at the constant 1 mm per year known for white-tailed deer (*Odocoileus virginianus*) (Hulbert, 1982), which share the browsing habit presumed for the low-crowned *Archaeohippus*. Uniformity of wear in fossil equids has been demonstrated in the past (Van Valen, 1964). Unlike Van Valen's (1964) sample of *Merychippus primus* or Voorhies' (1969) sample of *Protohippus cf. perditus*, there is no evidence of seasonality of death assemblages at Thomas Farm. Thus, I can not assume that each age class represents a cohort of births that occurred one year after the preceding age class. In the present study, the age of individuals must be estimated from tooth wear within each age class. This was complicated by the large degree of variation in initial crown height within the Thomas Farm sample. Variation in initial crown height exceeded estimated annual wear rate, a phenomenon observed by Van Valen (1964) for *M. primus* and *Pseudhipparion (=Griphippus) gratum.*

First Reproduction in Modern Females

Some feral mares (*Equus caballus*) of the Granite Range of Nevada produced offspring at two years of age (Berger, 1986). Relative to other *Equus*, this was unusually early, and was suggested to correlate with a period of rapid population growth, possibly in response to the removal of cattle from the region. Pregnancies were detected in 72% of yearlings in a Wyoming population (Wolfe et al., 1989). However, the authors of this study suggested that the method used to detect pregnancy in most study animals (measurement of progesterone levels) tended to greatly overestimate pregnancy rate.

Observations of subsequent foaling by these yearlings were not included in their study. In other studies cited by Berger (1986, also Garrott and Taylor, 1990), the earliest age of first reproduction for feral mares was three years. Density dependent increases of foaling rates were observed in the study of Garrot and Taylor (1990). Mares 3-5 years old experienced an increase in foaling in response to a 51% population decrease during the previous winter, however, 2-year-old mares were not observed to foal. According to Klingel (1969), mares of the Plains zebra (*E. burchelli boehmi*) attain puberty and exhibit mating behavior between 13-15 months, but do not deliver a foal until approximately 3.5 years. Considering the typical equid gestation length of 11-12 months, conception approximately correlates with the eruption of the second molar at 2 years (Sisson, 1927), whereas first foaling correlates with the eruption of the third molar at 3.5-4 years (Sisson, 1927).

Litter sizes in extant perissodactyls very rarely exceed one embryo per pregnancy (Millar, 1981). Multiple ovulations are common in *Equus*; multiple births are not (Stabenfield and Hughes, 1977). Therefore, discrimination against additional ova after one is fertilized must be a characteristic of equids (at least extant equids).

However, according to Bunnell (1987, p. 146), "(i)t is possible that the browsing habitat ...encourages multiple births," at least in artiodactyls, as a consequence of the furtive juvenile defense tactics available in that habitat. Litter size is negatively correlated with adult weight in eutherian mammals (Eisenberg, 1981; Millar, 1981); therefore, it is possible that the present limit on perissodactyl litter size is a consequence of large body size in all extant perissodactyls. Twinning is more common among small artiodactyls such as muntjacs and chevrotains than among large artiodactyls (Walker, 1964); the Chinese water deer (*Hydopotes inermis*) bears litters of four to seven young. Multiple birth litters are very common among species of hyrax (Sale, 1969), which is believed to be the extant sister taxon of the Perissodactyla (Fischer, 1989). These points raise the possibility of multiple births in populations of small, forest-dwelling three-toed horses. However, without more direct evidence of multiple births in ancient equids, the impact of multiple births on the fecundity of *Archaeohippus* will not be pursued beyond the observation that fecundity in the present study could be underestimated.

The modern perissodactyl reproductive pattern may not be an example of "phylogenetic constraint," but is instead an artifact of the recent evolutionary history of the group, a combination of allometric constraint and reduced diversity of perissodactyls in modern faunas. It is likely that gestation length in *Archaeohippus* was less than the 11-12 months of *Equus*. In environments without pronounced seasonal availability of resources, births need not be seasonal. Thus, even if *Archaeohippus* produced only one offspring per birth, with short gestation and year-round reproduction it is possible that a reproductive output estimate of one offspring per year may be an underestimate.

Thus, the assumption of this study is a mean reproductive output of up to one offspring per female per age class from age of first reproduction, even though the duration of each age class is estimated at 7 months (see Results). The actual calculation of these rates is also presented in the Results section.

First Reproduction in Modern Males

Fertility in male equids occurs by about 3 years of age (between the eruptions of M2 and M3), but age of first reproduction for males is somewhat later than in females, approximately 5 years (Klingel, 1969; Berger, 1986), which corresponds with the eruption of the canine teeth (4-5 years according to Sisson, 1927). In species of *Equus*, access to females is limited to dominant males, and is often resolved between males by threat display and combat, which can involve the canines (Klingel, 1969; Eisenberg, 1981; Berger, 1986). In the Granite Range study (Berger, 1986), males aged 7 - 10 years were more successful at intraspecific conflict than older and younger males. Even though birth ratios indicate a bias toward male births (1.3:1.0), adult ratios indicate a reduction in the proportion of males to females (0.76:1.0) (Berger, 1986). At least part of this male attrition must be due to the cost of intraspecific competition, including mortality and emigration of males in search of available females. Fecundity estimates for the population of *Archaeohippus* from Thomas Farm should include adjustments for a shift of sex ratios if evidence for such a shift exists in the data.

Results

Average crown height loss on m1 from Classes 3-5 is 1 mm. According to Hulbert (1984), this is the annual cheek tooth wear rate for a browser. Comparisons of average crown heights at different classes reveals a consistent pattern. Class 4 p4 crown height is 5.5 mm and Class 8 p4 crown height is 2.5 mm. Class 4 m3 crown height is 5 mm and Class 8 m3 crown height is 2.5 mm. Class 9 did not differ substantially from Class 8 in crown loss. Thus, between classes 4 and 8, the oldest *A. blackbergi* lost approximately 3 mm crown height from p4 and approximately 2.5 mm crown height from m3.

Greatest longevity for individuals in the sample can be estimated as follows: Average dp2 total crown height loss (representing tooth wear during Classes 1-3) = 1.2 mm plus average p2 total crown height loss (Classes 4-9) = 3.96 mm yields a total of 5.16

mm for Classes 1-9. Addition of average dp2 total crown height loss (Classes 1-3) = 1.2 mm plus average m1 total crown height loss (Classes 2-9) = 4.34 mm yields a total of 5.54 mm. So, based on ~1mm loss/year, these two estimates give a maximum observed life expectancy of ~5-5.5 years for the population of *A. blackbergi* from Thomas Farm.

Table 6. Estimated durations of age classes in *A. blackbergi*, *P. leonensis* (from Hulbert, 1984), and *E. caballus* (from Sisson, 1927) based on eruption sequence and tooth wear. No wear criteria have been devised to determine Classes 6+ in *E. caballus*.

	A. blackbergi Age (years)	*P. leonensis* Age (years)	*E. caballus* Age (years)
Class 1	0 – 0.6	0 – 0.5	0 – 1
Class 2	0.7 – 1.2	0.6 – 1.2	1 – 2
Class 3	1.3 – 1. 8	1.3 – 2.2	2 – 3
Class 4	1.9 – 2.4	2.2 – 2.8	3 – 4
Class 5	2.5 – 3.0	2.8 – 3.5	3.5 – 4
Class 6	3.1 – 3.6	3.6 – 4.6	n/a
Class 7	3.7 – 4.2	4.6 – 5.6	n/a
Class 8	4.3 – 4.8	5.6 – 7.0	n/a
Class 9	4.9 – 5.4	7.0 +	n/a

Since the m1 erupts before the dp2 is lost, the lower of the two estimates may be the more accurate. An alternate estimate based on the tallest (relatively) unworn m1 at 6.34 mm (Class 3 specimen UF 19755) plus the ~1 mm crown height loss from dp2 by Class 3 divided by 0.98 mm annual wear yields a greatest potential longevity of 7.5 years, at which point the cheek teeth would be almost completely worn.

Estimation of age at which m3 erupts can be derived from dp2 loss from classes 1-3 of 1.2 mm + m1 loss from classes 3-5 of 1 mm as ~ 2.2 mm or 2.2 years.

There is a great amount of p2 wear associated with Class 4. This is the ontogenetic period when *A. blackbergi* sheds dp2-dp4, erupts p2-p4, and begins to erupt m3, so this range of wear may indicate that this is a longer interval than the rest. Or, it may be an indication that p2 erupts slightly earlier than p3/p4, and thus bears a greater overall wear in Class 4 than in later classes when it is accompanied by the p3/p4. The analogous eruption timing in *E. caballus* are (from Sisson, 1927), eruption of p2/P2 at 2.5 years, p3/P3 at 2.5/3 years, p4/P4 at 3.5/4 years (taken together these are equivalent to *A. blackbergi* Class 4), and eruption of M3 at 3.5-4 years. Therefore, the equivalent duration of this Class in *E. caballus* is approximately 1.5 years, with these notable differences: the premolars do not erupt as simultaneously as in *A. blackbergi*, and there is greater overlap in the timing of eruption of P4 and M3 in *E. caballus*.

The average wear per Class is ~0.6 mm, thus the average duration of a Class is 7.2 months. The durations of the Classes in *A. blackbergi*, *P. leonensis* (from Hulbert, 1984), and *E. caballus* (from Sisson, 1927) are given in Table 6. Dental eruption in *E. caballus* is delayed relative to eruption in the Miocene taxa. The first two age classes in *A. blackbergi* and *P. leonensis* are of approximately equal duration, with subsequent classes in *P. leonensis* ranging in duration from 0.6–1.4 years.

The life table (Table 3) includes:

N = the sample size; age class;

N(x) = number of specimens in each age class;

d(x) = N(x)/N*1000, the proportion of the adjusted population that dies during class x;

l(x) = population size at the beginning of class x;

m(x) reproductive output of the population during class x;

l(x)m(x) = number of offspring born to the population during Class x;

q(x) = the proportion of mortality in Class x; duration of Class x;

e(x) average life expectancy for individuals alive in Class x. It is calculated as e(x) = (0.5duration(x)*d(x) + 1.5duration(x+1)*d(x+1) + 2.5duration(x+2)*d(x+2) ...until the oldest Class in the population)/l(x). Thus, for Class 7 of Table 3 e(x) = (0.3*51.72 + 0.9*68.97+1.5*51.72)/172.41 = 0.9 years.

Mortality bias against males creates a percentage of females in Classes 4-9 estimated at 58% based on data from Berger (1986). Rate of reproduction in Class 4 females is low, 11-25%, mean = 18% in various studies cited by Berger (1986), and with females accounting for 58% of the population, Class 4 fecundity [m(x)] is estimated at 0.18*0.58=0.104. Using further estimates derived from Berger (1986), births per female increase substantially in the later classes, so Class 5 m(x) = 0.5*0.58=0.29, while for Classes 6 and higher m(x)=0.7*0.58=0.406.

Estimated average longevity is highest for Class 1 (2.7 years). No individuals of this Class were found in the sample, and no estimate of mortality was made. Any mortality that I may have estimated for Class 1 would have compounded the problem of low estimated fecundity (see below). Thus, for the purposes of this analysis, all individuals in the population of *A. blackbergi* from Thomas farm had an average life expectancy of 2.7 years in Class 1. Average longevity for the population drops during Class 5 in response to a large increase in mortality in that class.

In addition to the standard survivorship curve, a particularly informative graphic display of life table data is the mortality curve (Dittus, 1975). This is especially true with life tables derived from fossils, because fossil assemblages directly inform us of within-class mortality. Fecundity, total life expectancy, etc., must be estimated, but mortality is well represented in all classes but those subject to taphonomic bias (e.g. delicate-boned neonates). The curve for *A. blackbergi* from Thomas Farm (Fig. 8) indicates that

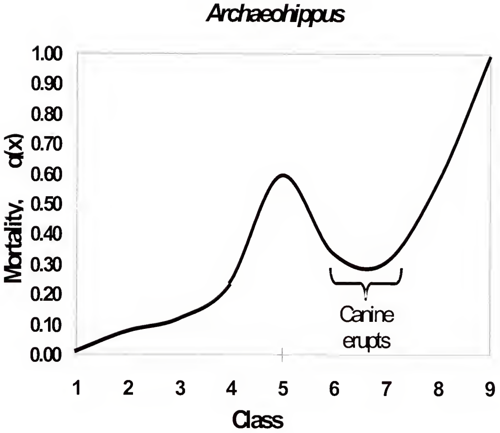


FIGURE 8. Age-specific mortality curve for *Archaeohippus blackbergi* from the Miocene Thomas Farm fossil site of Florida. Note the large increase in mortality at Classes 4 and 5, which may be the consequence of male combat for access to females. This is followed byh a reduction in q(x) in the middle-adult classes, indicating that most individuals that survive the mortality spike will survive to old age.

mortality is very high in Classes 4 and 5, which correspond with the early phase of sexual maturity.

Discussion

Estimates of First Reproduction in Fossils

In modern horses, the eruption of the second permanent molar (Class 3) occurs at about 2 years, the second premolar erupts at 2.5 years (Class 4) and the eruption of the third permanent molar (Class 4-5) occurs at about 3.5 to 4 years (Sisson, 1927). As stated above, in a rapidly growing population of feral *E. caballus*, early reproduction was observed to occur in two-year-old mares (which, corresponds to dental Class 3-4 of this study), with typical first foaling occurring among three-year-olds (Class 4-5). Based on tooth wear, the approximate age range of *A. blackbergi* during Class 3 was 1.3-1.8 years, Class was 4 1.9-2.4 years, and Class 5 was 2.5-3.0 years (Table 6). If the correlation between tooth eruption and reproduction as seen in *Equus* were present in *A. blackbergi*, then age at which precocious *A. blackbergi* females would deliver their first foal would be ~1.5 years, and age of normal first foaling would be 2-2.5 years.

As stated above, in *Equus*, although physiological reproductive maturity is attained in Classes 4-5, access to females is denied males until about Classes 6-7 (coinciding with the completed eruption of the canine), with best success attained at ages 7-10 years (Berger, 1986). This has bearing on the increased mortality seen in Classes 4-5 in Fig. 8 (see below).

Estimated fecundity for this sample replaces only 52% of the original population. This is may be due to: a) an age of first reproduction estimate that is too high; b) m(x) estimates that are too low, either because females were more successful at foaling, or sex ratios were more female-skewed than in populations of *Equus*; c) a combination of these factors.

During the calculation of l(x)m(x) it was assumed that births occurred in each of the adult age classes. This requires a gestation length of 7 months or less (a realistic assumption given the relatively small body size of the animals involved, *Equus* having a gestation of 11-12 months), virtually no interval between broods, and no breeding seasonality. This last is questionable given the strong correlation between estrus and photoperiod in *Equus* (Stabenfield and Hughes, 1977), although this may be a consequence of the year-long gestation of *Equus* and a need therefore to time both mating and parturition in the summer.

In life table analyses, if the estimated of age of first reproduction is too early, then estimated total fecundity of the population is too high. Inflated estimates of fecundity can in turn be adjusted for by artificially elevating mortality estimates in Class 1, as was done by Hulbert (1982, 1984). Total fecundity in the present study is low. The sum of all m(x)=2.02. Clearly, no single generation is solely responsible for maintenance of the population, and subsequent generations of females contribute contemporaneously with their immediate ancestors. However, these data suggest either that gestation is shorter than the average length of an age class; or that adult classes are underrepresented in the record from Thomas Farm; or that the durations of these later classes are greater than estimated (and are therefore able to accommodate more than one gestation per class).

Age Dependent Mortality

A comparison of the population dynamics of Thomas Farm *A. blackbergi* with Hulbert's (1984) study of *P. leonensis* demonstrates a fundamental difference between these sympatric equids. In the *A. blackbergi* sample, mortality in Class 4 is high (N = 11 of the original sample of 58). Mortality in Class 5 is higher (N = 22). The number of *A. blackbergi* individuals in the Thomas Farm sample that possess canine teeth (and therefore permit assignment to sex) is low. However, this peak (seen clearly in Fig. 8) in mortality mirrors a pattern of age dependent mortality observed in mammal taxa from feral horses (Berger, 1986) to monkeys (Dittus, 1975), and many others (see Mihlbachler,

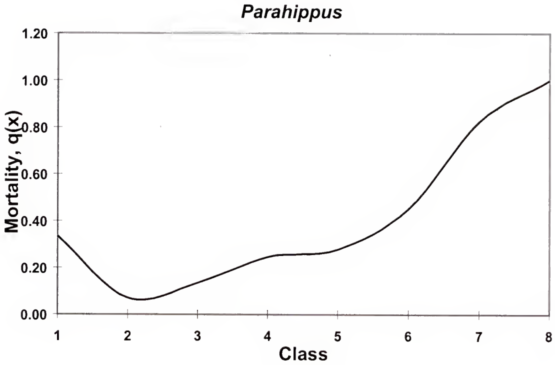


FIGURE 9. Age-specific mortality curve for *Parahippus leonensis* from the Miocene Thomas Farm fossil site of Florida. Mortality increases slightly in the mature classes, with highest q(x) in the oldest classes.

t2001, for a review). This mortality pattern indicates death due to wounds sustained by young males in battles over access to females with older, more experienced males.

While the *A. blackbergi* data show a dramatic increase in mortality at attainment of age of first reproduction (Classes 4 and 5), the *P. leonensis* age-specific mortality curve (Fig. 9) shows only a slight increase in mortality at this age, an increase that persists through Class 8. An intermediate pattern can be seen in the age-specific mortality curve of *Miohippus obliquidens* (Fig. 10), with a moderate increase in mortality at the start of the adult age classes.

In addition, using canine tooth size to identify the sex of specimens, Hulbert (1984) established that *P. leonensis* at Thomas Farm exhibits some sexual dimorphism in

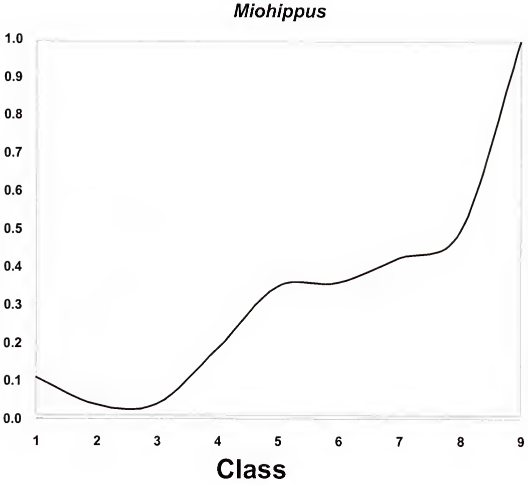


FIGURE 10. Age-specific mortality curve for *Miohippus obliquidens* from the Oligocene Harvard Fossil Reserve of Wyoming. Note the slight increase in mortality at Classes 4 and 5, with a continually high mortality in all subsequent age classes.

body size. *A. blackbergi*, while demonstrating dimorphism in canine tooth size, does not demonstrate body size dimorphism. For example, MCZ 3685 is a small individual (p4 apl = 9.7 mm; depth of jaw at p2 = 14.4 mm) with small canines (female). MCZ 7291 is a small individual (p4 apl = 10.0 mm; depth of jaw at p2 = 17.0 mm) with relatively large canines (male). MCZ 6997 is a large individual (p4 apl = 11.3 mm; depth of jaw at p2 = 19.4 mm) with small canines (female). The p4 apl of MCZ 6997 is 16% larger than that of MCZ 3685 and 13% larger than that of MCZ 7291, and the mandibular depth beneath the p2 is 35% larger and 14% larger, respectively.

In studies of modern ungulates, it has been suggested that annual competition for females selects for larger body size in males (Eisenberg, 1981; Janis 1982). However, this probably holds true for animals that use their entire body weight in attacks with horns or antlers. Hornless ungulates such as equids and chevrotains use their teeth (and, more recently in horses, their hooves), and are characteristically dimorphic in canine size and monomorphic in body size (Eisenberg, 1981).

Age/sex dependent mortality and sexual dimorphism in fossil and extant ungulates have been examined in detail by Mihlbachler (2001), who emphasizes that any attempt to interpret social behavior in fossil perissodactyl populations is handicapped by the relictual status of modern perissodactyl taxa.

Neonate Mortality Estimates

Due to their small size and undermineralization, bones of neonates are fragile and are characteristically under-represented in a fossil assemblage. Hulbert (1982) expected first-year mortality in *Neohipparion* to be nearly as high as that seen in modern savanna dwelling zebra, and adjusted Class 1 of his study to accommodate a large loss (55.9%). A similar correction was calculated for Thomas Farm *Parahippus* to give a first-year mortality of 41% (Hulbert, 1984). This was necessary to reduce total fecundity (productivity) in later classes to balance with the original population estimate of Class 1.

However, such a large adjustment may not be necessary. A number of studies of feral horses and white-tailed deer (*Odocoileus virginianus*) have shown first-year mortality can be less than 10% (Berger, 1986; Bunnell, 1987; Garrott and Taylor, 1990;

although, see Smith et al., 1996 for very high neonate mortality [>50%] for white-tailed deer in a wet prairie). These authors suggest that the high mortality in African studies is related to the extreme seasonality of water availability in the African savanna. Instead of increasing juvenile mortality in the life table, one can reduce total fecundity by pushing back the age of first foaling to accommodate the late age of first reproduction and lengthy gestation typical of perissodactyls. In the present study, this reduces fecundity to such a degree as to create an inadequate reproductive output, as discussed above. Increasing neonate mortality only exacerbates the problem of insufficient reproductive output.

Estimates of Average and Potential Longevity

Van Valen (1964) estimated potential longevity for the early Miocene equid *Merychippus primus* (~10 years) and middle Miocene equid *Pseudhipparion gratum* (~11 years). These are surprisingly similar, considering the cheek teeth of *P. gratum* are approximately 1.5 times the height of the cheek teeth of *M. primus*. The close correspondence in longevity appears to be the result of an increase in the rate of tooth wear in the younger taxon, probably the result of an increase in the amount of grass in the diet of *P. gratum* relative to the diet of *M. primus*. Thus, with its more abrasive diet, *P. gratum* needed taller teeth than *M. primus* in order to live ~1.1 times as long as *M. primus*.

A very similar relationship is seen in potential longevity in the sympatric horses from Thomas Farm. Hulbert (1984) estimated annual cheektooth-wear rates between 1.75 mm and 2.1 mm and potential longevity between 8.2 and 9.6 years for *P. leonensis*. The present study estimates annual cheektooth-wear rates of 0.98 mm and potential longevity of 7.5 years for *A. blackbergi*. Although the rate of tooth wear for *P. leonensis* is estimated at nearly twice that of the rate for *A. blackbergi*, the potential longevity of the former is approximately 1.09 – 1.28 times that of *A. blackbergi*.

The greatest average longevity in the Thomas Farm sample of *A. blackbergi* is found in Class 1 at 2.7 years. In Thomas Farm *P. leonensis*, greatest e(x) is 4.06 in Class 2; including the 0.5 years from Class 1 the greatest average longevity = 4.56 years. Thus, average potential lifespan of *P. leonensis* was 1.7 times that of *A. blackbergi*. This difference is a consequence of the very different mortality patterns of *A. blackbergi* and *P. leonensis* discussed above, which may indicate different modes of social organization in these two taxa, or differences in the spatial distributions of sex- and age-based mortality relative to the formation of the Thomas Farm fossil site. The fossil sample of *P. leonensis* may be more representational of the ancient living population of that taxon than is the sample of *A. blackbergi* of its original population (see below).

Paleoenvironmental Reconstruction of the Thomas Farm Fossil Site Based on Interpretations of Social Structure

Hulbert (1984) suggested that the Thomas Farm environment was completely forested, based on his reconstruction of the social structure of *P. leonensis* as being similar to that of forest-dwelling deer. However, this social structure may have persisted in *P. leonensis* even after its subsistence base had shifted toward more open country. Herding and harem defending as seen in some species of modern *Equus* may be relatively recent innovations. These are not at all typical reproductive strategies in burros (*E. asinus*) (Eisenberg, 1981). In addition, objections raised above as to the interpretation of social dynamics in extinct perissodactyl species apply to the question of using those interpretations for environmental reconstruction. The evidence of male combat is not informative, as such behavior is exhibited by harem-maintaining modern *Equus* in open country (Berger, 1986) as well as by more solitary deer in forests (Eisenberg, 1981).

Paleoenvironmental Reconstruction of the Thomas Farm Fossil Site Based on Interpretations of Dietary Preferences

A. blackbergi from Thomas Farm is represented by far fewer specimens (MNI = 58) than is *P. leonensis* (MNI = 89). This suggests that the locality was on the periphery of the local geographic range of *A. blackbergi*, but central to the local range of *P. leonensis*. This implies that Thomas Farm should be reconstructed as a partially open environment (as suggested in MacFadden, 1992) where the more hypsodont *P. leonensis* (which, according to Hulbert [1984] may have had a diet of both leaves and grasses) would dominate. The less frequent presence of browsing ungulates such as the equids *Archaeohippus blackbergi* and *Anchitherium clarencei*, two very rare rhinoceroses, and several species of very rare artiodactyls indicates that this area, though not a closed forest, perhaps was near one. Sinkholes in modern Florida usually support substantial vegetation including trees, even in open, dry areas. Browsing ungulates may have occasionally traveled to these forest isolates from larger stands of forest. With this the case, one would predict that the *Archaeohippus* population at Thomas Farm (those animals that died there) would not be a sample from the central population, but from the peripheral population. As stated above, those animals more likely to be so marginalized are lone males not yet skilled in intraspecific combat, which may have perished as a result of wounds sustained in such combat elsewhere.

Conclusions

This study of *Archaeohippus blackbergi* from Thomas Farm adds to the body of knowledge concerning the largest early Miocene terrestrial fossil site in the eastern United States. It provides an interesting contrast with Hulbert's (1984) study of the sympatric equid *Parahippus leonensis*. These populations differ in mortality profile as demonstrated by plotting age-specific mortality [q(x)]. As interpreted here, this is suggestive of greater mortality due to intermale combat in the population of *A. blackbergi*. These different mortality profiles may also indicate differences in spatial patterns of mortality, with *A. blackbergi* at Thomas Farm primarily represented by marginalized individuals—young males who succumbed to combat-induced physical trauma--and *P. leonensis* represented by a more complete population.

These sympatric equids are also distinct in the estimated rate of tooth wear (indicative of a less abrasive diet in *A. blackbergi*) and in the duration of age classes shorter in *A. blackbergi*). Potential longevity for these two taxa are quite close (as a consequence of the lower rate of tooth wear in *A. blackbergi*), although average longevity of *A. blackbergi* is much less than that of *P. leonensis* (as a consequence of the large amount of mortality in Classes 4 and 5 in *A. blackbergi*).

The mortality pattern of *M. obliquidens* from the Oligocene of Wyoming more closely resembles that of *P. leonensis*. Assuming that spatial bias in mortality assemblages is not an overwhelming factor in this pattern, the possibility arises that the difference in age-specific mortality indicates a biologically significant difference. One possibility is that male intraspecific competition was more ritualized in *M. obliquidens* and *P. leonensis*. Another possibility is that *A. blackbergi*, with its relatively large head and canines, was capable of inflicting more serious wounds on conspecifics than were the larger taxa.

This study demonstrates differences in population dynamics between closely related sympatric ungulates, including the probable presence of intense male intraspecific competition in the population of *A. blackbergi*. It adds to the growing body of published analyses of population dynamics of fossil mammals that add to our knowledge of the evolution of mammalian ecology, life history, and social behavior.

CHAPTER 4
STABLE ISOTOPIC ANALYSIS OF EVOLUTIONARY HETEROCHRONY, BODY SIZE REDUCTION, AND DIETARY SPECIALIZATION IN *ARCHAEOHIPPUS BLACKBERGI* FROM THE MIOCENE THOMAS FARM FOSSIL SITE

Introduction

The adaptive radiation of grazing horses of the subfamily Equinae during the middle Miocene of North America is a well-studied macroevolutionary phenomenon that resulted in at least 11 late Miocene clades. It demonstrates the coevolution of an ungulate lineage and its environment (Webb and Hulbert, 1986, MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991; MacFadden, 1992; Hulbert, 1993; Webb et al., 1995). Reduction of the side toes, elongation of distal limb elements, and increase in tooth crown height and occlusal complexity apparently are ungulate adaptations to life in open country (Kowalevsky, 1873; Marsh, 1879; Simpson, 1951). These trends suggest large-scale environmental change in much of North America during the Miocene, from a mosaic woodland/grassland habitat to expansive grasslands (Janis, 1976; Behrensmeyer et al., 1992; Janis et al. 1994). Although fossil grasses are known from the early Cenozoic, they are not widespread in North America until the Miocene. Their effect on ungulate dentitions becomes pronounced as numerous fossil lineages demonstrate coevolution with this expanding resource (Stebbins, 1981, MacFadden, 1997).

The Thomas Farm fossil site offers an opportunity to study the effects of this continent-wide environmental shift on early Miocene (Hemingfordian Land Mammal Age) equids in southeastern North America. Three equid taxa are present. All belong to a grade of horses called anchitheres, the members of which all have a molarized P2/p2 and lack high-crowned cheek teeth. Thus, this group contains *Mesohippus*, *Miohippus*, *Kalibatippus* and the anchitheres sensu stricto (*Anchitherium*, *Hypohippus*, *Megahippus*, and *Sinohippus*), *Desmatippus* (*Anchippus*), *Parahippus*, and *Archaeohippus*. The large, brachyodont equid *Anchitherium*, which, although common in Eurasia, is rare in the North American record, including the record from Thomas Farm. Its teeth and feet primitively resemble those of the genus *Mesohippus* from the Eocene-Oligocene, only much larger (Sondaar, 1968; MacFadden, 2001). *Archaeohippus blackbergi* from Thomas Farm is a small, short-crowned (brachyodont) equid. The genus *Archaeohippus* demonstrates phyletic body size reduction (MacFadden, 1987). At approximately 20 kg (Janis et al., 1994; although see MacFadden 1987 for an estimate of 44 kg), the estimated body mass of *A. blackbergi* is about half that of species of *Miohippus*, the common equid of the late Oligocene. Dwarfing lineages, which contradict Cope's Rule (Stanley, 1979; Jablonski, 1987), have been demonstrated in several groups of horses (MacFadden, 1987). *Parahippus leonensis* is intermediate in size, with mesodont teeth. Members of the genus *Parahippus* display the earliest expression of the suite of dental and postcranial adaptions characteristic of the Equinae, usually interpreted as open-country adaptations. The most derived states of these characters among parahippines are present in *P. leonensis*, a fact that accounts for the designation of this taxon as the outgroup of the middle Miocene radiation of grazing horses (MacFadden and Hulbert, 1988, Hulbert and MacFadden, 1991).

Archaeohippus is sympatric with *Parahippus* in the Hemingfordian faunas of Thomas Farm in Florida (Simpson, 1932), Garvin Gully in Texas (Hay, 1924), Pollack

Farm of Delaware (Emry and Eshelman, 1998), and the John Day fossil beds in Oregon (personal observation). Where both of these taxa are numerous, *Anchitherium* is rare. Sympatric ungulates partition food resources according to body size (Bell, 1971; Clutton-Brock et al., 1982; Osborne, 1984; Illius and Gordon, 1987). Thus, while the *A. clarencei* was a large-bodied browser that probably lived in forests (as indicated by their browsing dentitions and primitive manus and pes), and *P. leonensis* was a mixed feeder that included grasses in its diet, *A. blackbergi* was perhaps able to sustain itself on patchy browse on forest fringes and in riverine habitats. This last niche was previously occupied by only a few exceedingly rare artiodactyls (Webb et al., 1995). It appears that during the early Miocene, horses were quick to exploit the new habitats that arose with the fragmentation of the forests (Webb, 1977; Behrensmeyer et al., 1992) that had dominated North America throughout the Paleocene and Eocene.

The purpose of this study is to identify the mechanism of body size reduction in *Archaeohippus*. Body size evolution is the result of altered ontogenetic trajectories, or evolutionary heterochrony. Evolutionary heterochrony in fossil taxa can be studied directly through the analysis of stable isotopes of oxygen (Jones and Gould, 1999). At issue here is not merely a change of body size, but potentially also changes in diet and life history. A study of the population dynamics of *A. blackbergi* as compared with *P. leonensis* and *Equus caballus* (Chapter 3) yielded estimates of first foaling for *A. blackbergi* at 2-2.5 years, about 0.3 years earlier than in *P. leonensis*, and one year earlier than in modern *E. caballus*.

Heterochrony Affects Morphology, Life History, and Behavior

Hall and Miyake (1995, p. 35) define evolutionary heterochrony as a "change in the relative time of appearance of a character in a descendant relative to its time of appearance in an ancestor." Modification of ontogeny has been cited by many authors as a pervasive mechanism for morphological transformation in documented ancestor-descendant lineages.

Heterochronic morphological change in a descendant can be of two kinds: peramorphic, when the reproductively mature form of the descendant is hyper-adult (in size, morphology, or both) in comparison to its ancestor; and paedomorphic, when the reproductively mature form of the descendant is sub-adult in comparison to its ancestor. The actual mechanism involves the disjunction of the rate, onset, or offset of the development of individual structures or complexes in relation to each other (Alberch et al., 1979). The result is allometric change. If the rate or timing of maturation of reproductive tissue is changed in relation to that of the somatic tissue, the result would be a change of body size in the descendant relative to its ancestor, as sexual maturity is strongly correlated with a dramatic decrease in somatic growth rate.

Body size is strongly correlated with basal metabolic rate, life history, and diet (McNab, 1980, 1990; Eisenberg, 1981, 1990). Thus, a single heterochronic dwarfing event can affect each of these (McKinney and Gittleman, 1995). The ecological benefits of size reduction in *Archaeohippus* should include reduction of competition for resources with sympatric species. This is accomplished by placing taxa in different microhabitats in the subtropical woodland/savanna environment reconstructed for early Miocene Florida (MacFadden and Webb, 1982).

As stated above, individuals of the Miocene horse genus *Archaeohippus* are smaller than members of the Oligocene genus *Miohippus*, the closest outgroup genus to the clade that contains *Archaeohippus* (see Chapter 5). This is an example of phyletic dwarfism. Phyletic dwarfism, in its broadest sense, is size decrease in ancestral-descendant lineages, and is a form of paedomorphosis. Such global body plan change is concomitant with change in diet, life history variables such as age of first reproduction and longevity, and population structure (Eisenberg, 1981), probably due to the effect of common selective forces (Millar and Hickling, 1991). It is the result either of the process called neoteny, where somatic growth is retarded and sexual maturity is not; or of progenesis, where somatic growth rate is unchanged but sexual maturation rate is accelerated, causing an early onset of sexual maturity. A third paedomorphic process is post-displacement, which is delayed development of a particular structure (Alberch et al., 1979).

Either neoteny or progenesis could result in a descendant with adult body size smaller than that of its ancestor. The difference between these two processes is in the amount of time required for the descendant to attain adulthood. This has important evolutionary and ecological implications. With a reduction in body size due to heterochrony, other variables may be affected, including:

Diet. In either case, a dwarf species would be displaced in certain aspects of its ecology from that of its larger sister taxon. Diet of herbivores is partitioned among body size classes. Larger mammals have absolutely larger digestive tracts that can more thoroughly digest food simply because of the greater amount of time required for food to pass through the system (Janis, 1976). Therefore, larger herbivores are capable of subsisting on large quantities of poor-quality food, and are good indicators of environments with a year-round dependable supply of low-quality herbage such as grasses and woody plants. Smaller herbivores are capable only of processing smaller amounts of food, and so are dependent on higher quality herbage. However, they are well-suited to survive in environments with a dry season during which resources are available only in small patches, and are thus good indicators of such environments (Ravosa et al., 1995).

Reproduction. Studies have shown that, within a particular mammalian order, age of reproductive maturity correlates with body size (Eisenberg, 1981; McNab, 1990). However, in the case of neoteny, although body size is reduced, age of first reproduction is maintained at the point set in the ontogeny of the larger ancestor. Therefore, only members of a dwarf species that results from progenesis will be able to reproduce at an earlier age. If individuals of this species are as long-lived as their ancestors, their potential reproductive output will increase. Given equal initial population sizes and similar mortality rates, even if longevity is shortened, the population of progenetic horses as a whole would increase more rapidly than the population of the larger sympatric horse that reproduces later in life. This would provide at least short-term reproductive advantage to the progenetic species in displacing larger species from habitats with patchy high quality herbage. The discovery that *Archaeohippus* was a progenetic horse might, in part, explain the successful expansion by this genus into new habitats during the early Miocene.

Stable Isotopes in Tooth Enamel Archive Environmental and Behavioral Data

Evidence of progenesis would be a reduction in age of first reproduction between Archaeohippus and Miohippus. Jones and Gould (1999) demonstrated neoteny in certain lineages of the Jurassic bivalve Gryphaea. Studies of heterochrony rely on accurate estimates of absolute age in specimens, such as are available from stable isotope analysis.

Age of first parturition in modern equids is strongly correlated with eruption of the third molar (Sisson, 1927; Berger, 1986). Unless this correlation is a recent innovation in equids, it should be possible to estimate age of first reproduction in fossil horse populations by determining the timing of the eruption of the m3. If this ontogenic event required the same amount of time in *Miohippus* and *Archaeohippus*, then neoteny was the process responsible for size reduction in *Archaeohippus*; if timing of this event is reduced in *Archaeohippus*, the process involved is progenesis.

Previous studies of mammal tooth enamel have demonstrated that it is a faithful archive of environmental oxygen isotopic ratios ($\delta^{18}O$), particularly those of dietary water (Fricke and O'Neil, 1996). Oxygen isotope ratios of water reflect the temperature of the environment at the time the water was precipitated (Mazor, 1991). Horse cheek tooth enamel is deposited in regular increments, visible as horizontal bands. Each growth increment preserves the isotopic ratio of meteoric water ingested during that growth period (Fricke and O'Neil, 1996).

Stable isotope analysis of equid tooth enamel has been used to interpret ancient climate, environmental evolution, and feeding ecology (MacFadden et al., 1996; MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; MacFadden et al. 1999; MacFadden, 2000). This technique detects the ratio of stable isotopes of oxygen ($\delta^{18}O$)

preserved in the regular growth increments of tooth enamel, an archive of seasonal isotopic variation (Fricke and O'Neil, 1996; Sharp and Cerling, 1998). An entire adult cheek tooth row p2-m3 contains the seasonal fluctuations experienced by an individual horse while the enamel of these teeth was mineralizing. Bryant et al. (1996a) performed a similar analysis with modern and Miocene equids, and Bryant et al. (1996b) analysed several species of *Mesohippus* and *Miohippus*. Both of these studies involved the analysis of one bulk sample per tooth. Both studies revealed seasonal patterns in $\delta^{18}O$ obtained from enamel phosphate. Three patterns were found in the Oligocene equids analysed by Bryant et al. (1996b) which suggested interesting differences in both birthing seasonality (spring versus fall births) and developmental timing (12 months vs. 18 months for eruption of the m3). Interestingly, intraspecific variation in duration of tooth mineralization was as great, in some instances, as was intergeneric variation.

Stable isotopes may also be used to elucidate dietary specialization in *Archaeohippus*. As stated above, when closely related mammal herbivore species are sympatric, they experience dietary displacement according to body size requirements. In the case of *Archaeohippus* vs. *Parahippus* seen at Thomas Farm, I had predicted that *Archaeohippus* would eat low-growing plants and bushes in the semi-open woodlands. In contrast, *Parahippus* would eat grass and leaves from taller plants and trees in the more open grasslands. There are systematic differences in the isotopic content of C3 plants due to conditions of growth. Plants that grow in the understory of forests have significantly more negative $\delta^{13}C$ (Buchmann et al., 2001). Systematic differences in carbon isotopes taken from fur samples from four species of New World monkey correlated with the degree of shade in their respective environments (Schoeninger et al., 1997). In addition, plants that grow within about 0.5 m of the ground in dense multistratal forests use air that is filled with CO_2 derived from decaying plant matter. Due to fractionation, C3 plants have a $\delta^{13}C$ ratio of about -27‰, far more negative than atmospheric $\delta^{13}C$ of -8‰. Therefore, low-growing plants available to small herbivores are isotopically depleted in $\delta^{13}C$ relative to high-growing plants (Farquhar et al., 1989; van der Merwe and Medina, 1989).

This study addresses two hypotheses: 1) progenesis, and not neoteny, was the proximate genetic/developmental mechanism responsible for body size reduction in the early evolution of *Archaeohippus*; and 2) dietary differentiation existed between sympatric equids at Thomas Farm and with *Miohippus*, with *Miohippus* browsing in closed forests, *Parahippus* consuming more open country and higher level (sun-drenched) plants, and *Archaeohippus* between these two. These hypotheses were tested with stable isotope analysis.

Materials and Methods

Three taxa were used in this study: *A. blackbergi* and *P. leonensis* from Thomas Farm, and *Miohippus obliquidens* from the Harvard Fossil Reserve of Goshen, Wyoming, a locality that dates from the early Oligocene (Orellan) (Schlaikjer, 1935; Prothero and Shubin, 1989). The latter taxon represents the outgroup that should have the plesiomorphic characterist states to be measured with isotopic analysis. Mandibles with m3 in early occlusion were selected from the Vertebrate Paleontology Collection of the Florida Museum of Natural History, University of Florida. Enamel was removed in a series of horizontal lines (Fig. 11) with a 0.8 mm dental burr attached to a Foredom variable speed drill with a flexible cable and a foot switch. Three lines of enamel were

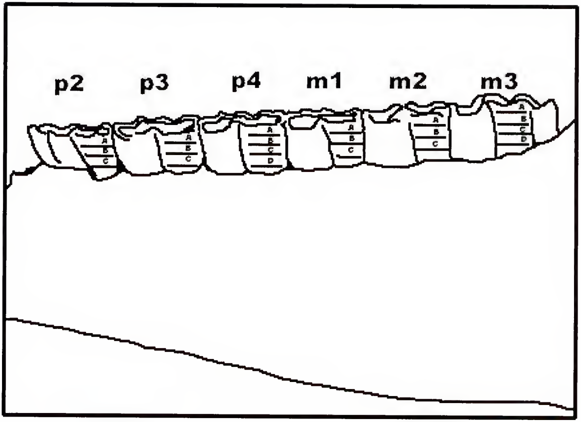


FIGURE 11. Diagram depicting the tooth positions from which enamel samples were extracted. Abbreviations: p = lower premolar; m = lower molar

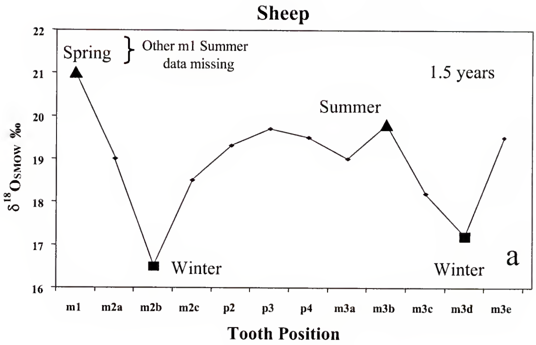
removed from each p2, p3, m1, and m2, while 4 lines were removed from each p4 and m3 due to the slightly greater height of these teeth.

The enamel powder was treated overnight with 35% hydrogen peroxide to remove organic contaminants. The hydrogen peroxide solution was decanted and the enamel was washed with distilled water before an overnight treatment with 0.1 N acetic acid to remove secondary calcite. Further washing of the powder with distilled water was followed with rinses of 95% methanol to dessicate the samples, which were left to dry overnight. The treated enamel powder was reacted with 100% phosphoric acid at 90°C for 90 minutes to produce carbon dioxide gas. This gas was moved through a vacuum line designed to trap water and non-condensible contaminants. The remaining gas from each sample was sealed in a glass tube with silver wool. These were kept at 60°C overnight to promote bonding of sulfur contaminants with the silver wool. These tubes were put in the ten port cracker manifold on the VG Micromass Prism II isotope ratio mass spectrometer in Dr. David Hodell's lab at the Department of Geology, University of Florida. The mass spectrometer was calibrated with the international standard NBS-19 (derived from limestone) and the in-house standard MeMe (elephant enamel).

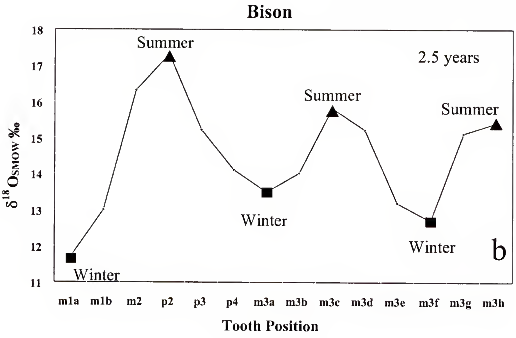
Using a sample structure similar to that of Fricke and O'Neil (1996), I selected 3 samples from m1, 2 from m2, 1 each from p2, p3, p4, and 4 from m3. In an equid, the m1 starts mineralizing in utero and finishes prior to weaning; thus the isotopic ratios of this tooth in any foal are influenced by the body water chemistry of its mother, which tends to enrich and compress the range of $\delta^{18}O$ in m1 (Bryant et al., 1996a, b). It is the only tooth among the permanent cheek teeth that archives this pre-weaning period. Mineralization of the premolars overlaps the later mineralization of the m2, which starts to mineralize during the weaning period (and which, therefore, may be isotopically enriched by mare's milk), and the early mineralization of the m3. Fricke and O'Neil (1996) used only one sample from each premolar to enhance resolution of this central growth period while avoiding redundancy. See Discussion and Fig. 12 for further details on this model.

Results

Each taxon exhibited cyclic variation in $\delta^{18}O$ and $\delta^{13}C$ (Figs. 13-17, Table 7). Within the Florida sample, these patterns can be detected:



(Derived from Fricke and O'Neil 1996)



(Derived from Fricke and O'Neil 1996)

FIGURE 12. Fricke and O'Neil's (1996) $\delta^{18}O$ data from the cheek teeth of a sheep (a) and a bison (b) showing seasonal cyclicity. High ratios interpreted as summer signals are indicated with ▲ and low ratios interpreted as winter signals are indicated with ■.

1. The oxygen plots for *Archaeohippus* I (Fig. 14a) and *Parahippus* II (Fig. 15b) are very similar in m1 growth pattern. Divergence in timing after this point indicates more rapid maturation in *Archaeohippus* I relative to *Parahippus* II.

2. The carbon plots for *Archaeohippus* I and II (Fig. 16, 17) show a summer peak at the same tooth position (p2). The curve for *Archaeohippus* I is more negative and contains more variance, but the overall patterns for *Archaeohippus* I and II resemble one another.

3. The oxygen and carbon plots for *Parahippus* I and II (Figs. 15a, 16, 17) are similar, but the seasonal shifts seen in the curve for *Parahippus* II occur earlier by 1 or 2 tooth positions.

4. The mean for *A. blackbergi* $\delta^{18}O$ is –0.4‰ and for *P. leonensis* is –1.4‰. Mean $\delta^{13}C$ for *A. blackbergi* is–10.7‰ and for *P. leonensis* is –11.1‰.

Patterns of oxygen and carbon variation within the Wyoming sample include:

1. Whereas the carbon and oxygen curves (Figs. 14-17) of the Florida equids track each other closely (e.g. the samples with the most positive carbon ratios also have the most positive oxygen ratios), the *M. obliquidens* ratios do not (Figs. 13, 16). When an oxygen curve becomes more positive, its corresponding carbon curve becomes more negative.

2. The two sets of oxygen data for *M. obliquidens* (Fig. 13) have similar patterns until they diverge in the m3 positions. Also, *Miohippus* II has a greater range of variation in $\delta^{18}O$.

3. The same can be said of the carbon data, except that the curve for later growth (m2 and m3) in *Miohippus* I is very flat, lacking the nearly 4‰ drop seen in *Miohippus* II

(Fig. 16). Detection of further resemblances/disparities is confounded by the high number of missing data for this taxon, a result of its very thin enamel.

Table 7. Stable isotope data for specimens in this study. Abbreviations used: Arch = *Archaeohippus*, Mio = *Miohippus*, Para = *Parahippus*.

Tooth	Arch I		Arch II		Mio I		Mio II		Para I		Para II	
Position	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$
m1a	-12.5	-1.7	-11.5	-1.1	-9.8	-3.0	-8.0	0.0	-11.3	0.7	-13.0	-4.8
m1b	-11.4	1.4	-10.7	-1.0	n/a	n/a	-8.2	-2.1	-10.7	1.4	-11.2	-1.2
m1c	-11.5	-1.5	-10.3	-0.6	n/a	n/a	-8.8	-3.2	-10.0	2.5	-12.0	-2.9
m2a	n/a	n/a	-10.3	1.3	-9.0	-5.3	n/a	n/a	-10.5	2.4	-11.0	-0.2
m2b	-11.6	1.0	-10.2	1.8	-8.8	-7.0	-8.1	-7.5	n/a	n/a	-12.6	-4.0
m2c	-10.8	1.6	-10.4	-0.6	-9.9	-4.1	-7.3	-6.4	-10.1	-0.2	-10.8	-1.1
p2a	-9.8	2.5	-9.3	-1.2	n/a	n/a	n/a	n/a	-10.0	-0.3	-12.2	-3.4
p2b	-10.4	2.0	-9.8	0.9	-11.4	-4.3	-8.2	-1.1	-10.6	-2.7	n/a	n/a
p2c	-10.5	-1.9	n/a	n/a	n/a	n/a	n/a	n/a	-10.0	-1.2	-10.4	-0.6
p3a	-10.4	1.3	-9.9	-1.0	-9.6	-4.8	-8.2	-1.4	-9.6	0.9	-13.4	-7.2
p3b	-15.1	-9.9	-9.9	-0.8	-8.6	-1.4	-8.0	-1.1	-11.1	-3.2	-13.3	-6.9
p3c	-8.9	4.3	-10.0	0.0	-9.4	-4.3	-8.3	-3.0	-9.8	0.3	-12.8	-5.2
p4a	-11.1	-0.6	-9.8	-0.6	-8.8	-4.4	-8.1	-1.7	-11.3	-2.2	-10.6	-1.9
p4b	-9.9	2.7	-9.9	-1.2	-9.4	-3.9	-11.3	-7.6	-10.1	0.8	-10.4	-1.8
p4c	-10.2	1.2	-13.1	-8.0	-9.3	-2.7	-11.5	-8.1	-10.4	-0.9	-10.6	-1.7
p4d	-9.8	2.3	n/a	n/a	n/a	n/a	n/a	n/a	-10.1	0.2	-11.3	-2.9
m3a	-12.5	-2.1	-9.9	-1.8	-8.9	-2.9	n/a	n/a	-11.9	-2.0	-11.3	-0.9
m3b	-10.9	1.0	-9.9	-0.2	-8.8	-3.4	-7.8	-8.0	n/a	n/a	-13.3	-4.2
m3c	-11.2	0.0	n/a	n/a	-8.9	-2.9	-7.7	-7.2	-10.1	1.2	-11.5	0.1
m3d	-10.7	-0.2	n/a	n/a	n/a	n/a	-8.4	-9.4	-10.5	0.4	-10.7	-0.9

Differences between the Florida and Wyoming samples include:

1. *Miohippus* has a lower oxygen range, with no positive ratios, and an average $\delta^{18}O$ of –4.2‰ which is 3.3‰ more negative than the average of –0.9 for the Thomas Farm $\delta^{18}O$ samples (Fig. 13).

2. The carbon isotope ratio for *M. obliquidens* has an average of –8.9‰, which is 1.5‰ less negative than the average of –10.4‰ $\delta^{13}C$ for the Florida taxa (Table 7, Fig. 13).

Discussion

Patterns of variation in $\delta^{18}O$

Figure 3 of Fricke and O'Neil (1996) depicts the periods of enamel mineralization in cattle and sheep. A comparison with eruption timing for these animals as listed in Sisson (1927) indicates that the key for Fig. 3 of Fricke and O'Neil (1996) has reversed the identification of the mineralization ranges of these taxa. Thus, sheep mineralize all of their cheek teeth by ~20 months, and cattle by ~30 months. Plots (Fig. 12) of the $\delta^{18}O$ data in Table 1 of Fricke and O'Neil (1996) reveal cyclicity that very closely approximates these estimates in both cases. Summer highs and winter lows differ by at least 2‰. Based on this criterion, I tentatively reject the possibility that the 1‰ drop at position m3a on the sheep plot (Fig. 12a) represents a winter low between adjacent p3 and m3b positions. Initial $\delta^{18}O$ readings in Fig. 2a are very high; this suggests a spring birth according to Bryant et al. (1996a, b). Fricke and O'Neil state that this sheep was, in fact, born in the spring. No further isotope ratios from the m1 were analyzed, so no summer signal (or lack thereof) can be discussed. Figure 12b starts with low readings, which Fricke and O'Neil (1996) interpret as being indicative of a fall birth for this bison. Modern American bison typically give birth in the spring (Walker, 1964). Estimating season of birth from these data is complicated by differential gestation length. Gestation in sheep requires approximately five months (Catchpole, 1977), whereas gestation in bison requires approximately nine months (Walker, 1964), a duration 1.8 times that of sheep gestation. Mineralization of teeth in cattle, which have a gestation rate similar to that of bison, requires about 30 months (postnatal growth), 1.5 times as long as mineralization in sheep (Fricke and O'Neil, 1996). The m1 of a sheep born in May probably began mineralizing in April and would contain a warm weather isotope signal. The m1 of a bison born in May probably began mineralizing almost one month earlier than that of a sheep, and would have an initial isotopic ratio that reflects much cooler weather. Both of these isotope plots may indicate spring births.

Using Fig. 12 as a model, the plot of $\delta^{18}O$ from *Miohippus* I (Fig. 13a) has a spring birth pattern with a 4‰ decrease from m1a to m2b (m1b and m2a are both missing data). A subsequent decrease between m2c and p3a does not achieve the ≥2‰ decrease criterion, so this is not considered to indicate a shift in seasons. If that is the case, then this plot describes one year from m1a to m3a, plus several months for the remaining m3 positions (sample m3d did not produce results; it might have contained a winter signal); perhaps 1.2 years in all. The pattern over the first half of Fig. 13b is very similar in that a spring or summer birth is followed by a clear winter signal, then a summer. However, in this case, the other half of the pattern includes two more summer signals followed by a very clear winter drop, thus indicating ~1.5 years. The variation between these two patterns (and others, as addressed below) may indicate intraspecific differences of developmental rates, and seem to be within normal ranges of variation for tooth mineralization and eruption, which can vary up to six months in modern *Equus* (Hillson, 1986; Bryant et al., 1996b). This variation may also indicate inaccuracy in the sampling strategy used in this study.

Figure 14 depicts $\delta^{18}O$ for *A. blackbergi* from Thomas Farm. The pattern for *Archaeohippus* I (Fig. 14a) indicates a fall/winter birth with three winter and three summer signals plus two additional positions. As the first signal may be derived from anytime between late fall and late winter, the period of time represented by m1a-m1b

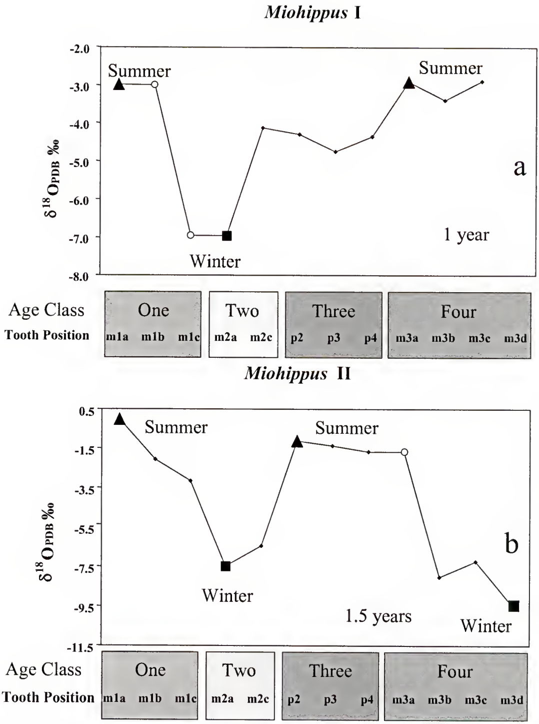


FIGURE 13. Plots of $\delta^{18}O$ for two specimens of *Miohippus obliquidens* from the Orellan Goshen Hole Harvard Fossil Reserve of Wyoming. In addition to the symbols for summer highs (▲) and winter lows (■), missing data that have been estimated for plotting purposes are indicated by ❍.

is indeterminate, but probably not a full 0.5 years. Thus, Fig. 14a can be said to depict ~2.5 years. However, it seems unlikely that mineralization of the m1 would actually require nearly one year, so this graph may represent 2 years. The pattern for *Archaeohippus* II (Fig. 14b) suggests a fall/winter birth that occurred earlier in the season, with three winter signals before the first summer signal. The rest of the pattern is less readily interpreted. The low point at the p2 position might be subsequent winter, with the signal from the p4 position representing the following summer, m3a the next winter, etc. However, the difference between p2 and p4 is <1‰, and the difference between p4 and m3a is <2‰. Therefore, the signal at position p4 is not (under my criterion) a summer signal, although m3b may be a summer signal. Further resolution of the pattern is unavailable, as positions m3c and m3d did not yield isotopic data. However, the data that are available suggest a somewhat shorter mineralization period, perhaps closer to 2.0 years.

The graphs in Fig. 15 depict $\delta^{18}O$ for *P. leonensis* from Thomas Farm. *Parahippus* I (Fig. 15a) has a fall/winter birth, three summer signals, two winter signals, and an indeterminate period of time before the first summer and after the third summer. This suggests a mineralization period of ~2.5 years. Figure 15b (*Parahippus* II) indicates a later winter birth followed by four summers and three winters. Therefore, tooth mineralization and eruption in *Parahippus* II required 3.0-3.5 years, again demonstrating variability in maturation rates similar to that seen in modern equids (Hillson, 1986).

Estimates of age of maturity and evidence of heterochrony. From the above analyses come these estimates of ontogenetic timing: *M. obliquidens* mineralized its cheek teeth in 1.0-1.5 years, *A. blackbergi* mineralized its cheek teeth in ~2.5 years, and

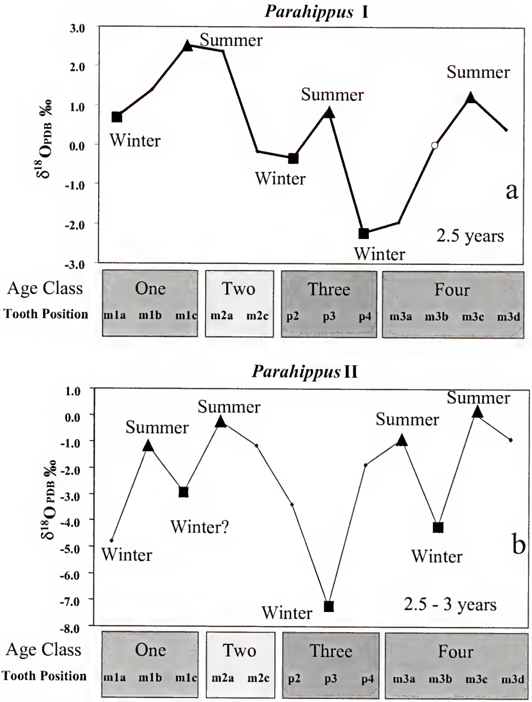


FIGURE 14. Plots of $\delta^{18}O$ for two specimens of *Parahippus leonensis* from the Hemingfordian Thomas Farm fossil site of Florida. Symbol usage as described in Fig. 13.

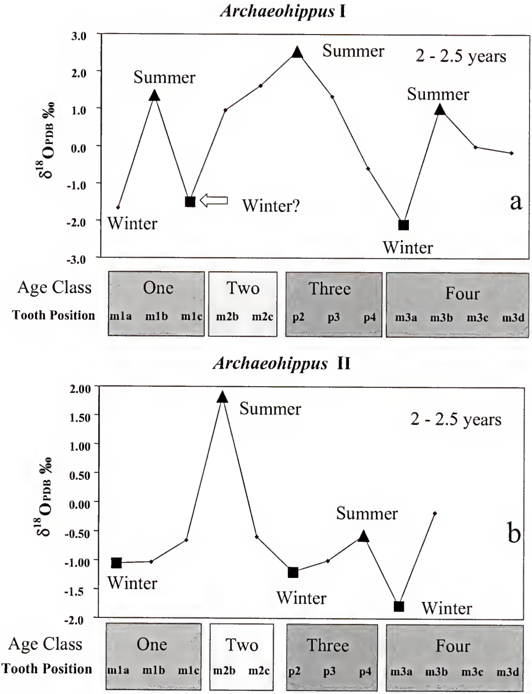


FIGURE 15. Plots of $\delta^{18}O$ for two specimens of *Archaeohippus blackbergi* from the Hemingfordian Thomas Farm fossil site of Florida. Symbol usage as described in Fig. 13.

P. leonensis mineralized its cheek teeth in 2.5-3+ years. The latter estimates correspond closely with estimates obtained from analysis of tooth wear (Hulbert, 1984; this study, Chapter 3). Both *A. blackbergi* and *P. leonensis* demonstrate an increase in developmental timing relative to *M. obliquidens*.

Estimates of mineralization rates for the Oligocene equids *Mesohippus sp.*, *Mesohippus westoni*, as well as one specimen of *M. obliquidens* obtained by Bryant et al. (1996b) range from 1.0-1.5 years. Therefore, *M. obliquidens* is in this study is typical of Oligocene equids in mineralization rate, as it is in body size. Thus, in the morphocline from the typical body size of the Oligocene equid as represented by *M. obliquidens* to the reduced body size of *A. blackbergi*, the latter can not be said to have undergone progenesis. In fact, developmental timing in *A. blackbergi* from the early Hemingfordian represents a significant increase over that of the Orellan equids used in this study and in Bryant et al. (1996b). These results contradict conclusions drawn by O'Sullivan (2000). Whether this increase is present in *A. mannulus* from the Arikareean of Florida can not be evaluated at this point because the sample of this species includes only one mandible which, being part of the holotype material, can not be sacrificed.

A note on extreme variation in δ^{18}O. Fricke and O'Neil (1999) demonstrated that correlation between δ^{18}O and temperature is weaker in Winter than in Summer, especially in lower latitudes. The specimens *Parahippus* II and *Miohippus* II have ranges of δ^{18}O in excess of 7‰ and 9‰, respectively. These δ^{18}O ranges indicate isotopic variability of source waters, and this variability is affected not only by temperature. Evaporation, humidity, and precipitation are linked to wet/dry seasonality in tropical environments (Swart et al., 1996), and with $CaCO_3$ input to groundwater, strongly influence source water chemistry in springs and spring-fed rivers.

Evaluating Dietary Differentiation in *A. blackbergi* and *P. leonensis*

While variation in $\delta^{18}O$ of tooth enamel in this study derives from environmental variability and its effects on dietary water, variation in $\delta^{13}C$ derives primarily from differential photosynthetic activity in C3 plants, including:

1. Decreasing (more negative) $\delta^{13}C$ ratios result from decreased light intensity (due to the plant growing in shade or during winter) and photosynthesis (Farquhar et al., 1989).
2. Carbon ratios decrease ~2-3‰ in the middle of the growing season, then recover, though usually not to early season highs (Leavitt and Long, 1982).
3. Leaves are 2-3‰ more negative than stems (Leavitt and Long, 1982).
4. Plant $\delta^{13}C$ values increase as water becomes scarce (Farquhar et al., 1989).
5. Plants that grow near the ground in forests experience depressed photosynthetic rates and utilize air that is very negative relative to normal atmospheric $\delta^{13}C$ due to input from decaying plant matter in the soil; both of these factors reduce $\delta^{13}C$ (van der Merwe and Medina, 1989; Buchmann, et al., 2001).
6. Short-lived perennials and deciduous forbs can be 5‰ more negative than long-lived plants (Ehleringer, 1993).

Body Size and Resource Partitioning

The adaptive radiation of the anchitheres involved the evolution of a variety of specialized forms from the low diversity genus *Miohippus* (MacFadden, 1987).

Fragmentation of North America forest habitats during the Oligocene produced abundant opportunities for anchithere populations to diversify (Webb, 1977). Once ecologically distinct populations were established, competitive interactions between newly sympatric populations would encourage further ecological and morphological differentiation (Mayr, 1963; Bock, 1970; Schluter, 1994).

Resource partitioning on a continental scale is determined by environmental factors. Some of the best studies of continent-wide interspecific dynamics come from Australia, where most large scale ecosystems are still intact. In one such study, the authors state that "[t]he extent of sympatry and allopatry appears to be determined by the independent reaction of each species to specific and differing climatic stimuli rather than by biological interaction between species" (Caughley et al., 1987, p. 751). In the study of Caughley et al. (1987), two species of grey kangaroo inhabit large geographic regions, each of which is characterized by a certain seasonal rainfall pattern. Sympatry occurs in a third region where seasonality of rainfall is minimal. The range of the red kangaroo is less restricted, corresponding to annual means of rainfall and temperature, not seasonality of these variables. There are considerable areas of overlap between these species, so this is not a case of competitive exclusion. Instead, it is a passive process of specialization that permits each species a unique habitat with sympatry in those areas where the climatic regimes intergrade.

On a local level, resource partitioning among sympatric ungulates of different body sizes is well known. In one study (Osborne, 1984), red deer and sheep selected mesotrophic (as opposed to oligotrophic - there were no eutrophic communities available) grass communities dominated by *Agrostis* and *Festuca*. Sheep spent more time on these grasses than either male or female deer. Stags usually selected oligotrophic pastures. In a study of habitat use by red deer in the absence of sheep (Clutton-Brock et al., 1982), both hinds and stags showed a much stronger preference for mesotrophic plant communities. Intensive grazing by sheep reduces the availability of grass. Stags, being largest and therefore having absolutely greater maintenance energy requirements, are the first to leave the company of hinds and sheep in search of taller, more easily procured foodstuffs in the oligotrophic plant communities. In a species of sexually dimorphic ungulate, the displacement of males toward oligotrophic plant communities agrees with a prediction made by Bell (1971) that larger herbivores will switch to poorer food sources before smaller herbivores do (Illius and Gordon, 1987). However, in the fossil fauna of Tarija, Bolivia, two of the smallest ungulates (*Lama* and cf. *Vicuna*) were grazers, while two of the equids, including the very large *Hippidion principale*, were mixed feeders. However, the C_3 component consumed by these equids may have been montane grasses, a possibility suggested by the fact that these are relatively short-legged equids that may have been adapted to mountainous terrain (MacFadden and Shockey, 1997).

Patterns of variation in $\delta^{13}C$

Figure 16 depicts $\delta^{13}C$ for all specimens in this study. All but three of the plotted values for *M. obliquidens* from Harvard Fossil Reserve, Wyoming are more enriched than all values plotted for the Thomas Farm taxa. This may indicate that the environment within which food plants grew was more arid and open than the environment of Thomas Farm. Although the Harvard Fossil Reserve is a rich bonebed that may have been a lake shore (Schlaikjer, 1935), the extensive nature of its fossil deposits may have been the result of severe seasonal drought conditions. By the Orellan, Wyoming was being impacted by the global cooling/aridification trend that originated near the Eocene/Oligocene boundary (Behrensmeyer et al., 1992; Berggren and Prothero, 1992; Evanoff et al., 1992). The hypothesis stated earlier in this study, that the stable isotopes of carbon of *M. obliquidens* would reflect a diet of plants grown in the shade of a heavy woodland, is not supported. The carbon isotope ratios of *M. obliquidens* are 1.5‰ more enriched than those of the Thomas Farm taxa, indicating more active uptake of heavy isotopes, possibly in response to drought stress (Farquhar et al., 1989). That the oxygen ratios of *M. obliquidens* are 3.3‰ more depleted than those of the Thomas Farm taxa may indicate a generally cooler mean annual temperature in Orellan Wyoming than in the Hemingfordian of Florida. Alternately, it may be a consequence of the continental effect, which is the phenomenon where cloud masses will lose their heavy isotopes to precipitation as they travel across a continent, with each successive precipitation event more negative than the last (Mazor, 1991). The continental effect would have been very limited in Florida during the Hemingfordian, when the peninsula was much more narrow than at present. Although isotopically depleted relative to seawater, the chemical composition of precipitation in Florida is strongly influenced by the surrounding seawater, as a result of integration of seawater aerosols that can move far inland (Upchurch, 1992).

Figure 17 depicts carbon curves for the Thomas Farm taxa. Primarily on the strength of the very negative ratios of *Parahippus* II, *P. leonensis* has an average $\delta^{13}C$ that is 0.4‰ more negative than the average $\delta^{13}C$ for *A. blackbergi*. Such a small difference does not support the hypothesis of dietary displacement between these taxa.

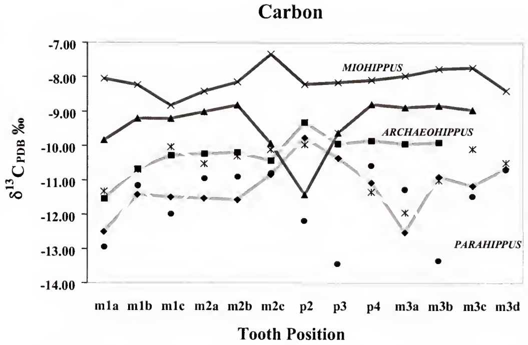


FIGURE 16. Plots of $\delta^{13}C$ for *Miohippus obliquidens* from the Orellan Goshen Hole Harvard Fossil Reserve of Wyoming and for *Archaeohippus blackbergi* and *Parahippus leonensis* from the Hemingfordian Thomas Farm fossil site of Florida. Symbol usage as described in the caption to Fig. 13.

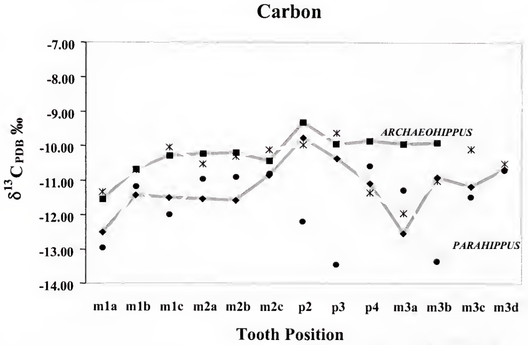


FIGURE 17. Plots of $\delta^{13}C$ for *Archaeohippus blackbergi* and *Parahippus leonensis* from the Hemingfordian Thomas Farm fossil site of Florida. Symbol usage as in Fig. 13.

However, samples sizes are small, and an analysis with more samples might detect ecological discrimination.

In the individual isotope ratio plots of *A. blackbergi*, δ^{13}C ratios increase as δ^{18}O increase (Table 7). This is a predictable reaction of leaf δ^{13}C to drought stress (Farquhar et al., 1989; Ehleringer, 1993). The pattern is reversed in *M. obliquidens* (Fig. 18), as it is in comparisons of mean δ^{13}C and δ^{18}O for both *A. blackbergi* and *M. obliquidens* (this is discussed further below). Mean ratios for *Archaeohippus* I are –0.7‰ δ^{13}C and +0.3‰ δ^{18}O relative to those of *Archaeohippus* II. Mean ratios for *Miohippus* I are –0.8‰ δ^{13}C and +0.7 δ^{18}O relative to those of *Miohippus* II. In both of these comparisons, those individuals with slightly less negative δ^{18}O have slightly more negative δ^{13}C.

Mean ratios for *Parahippus* I are +1.2‰ δ^{13}C and +2.6 δ^{18}O relative to those of *Parahippus* II. This difference may relate not to resource partitioning but to environmental/climatic differences affecting individuals which may have lived hundreds or thousands of years apart. However, it is tempting to interpret these results in terms of possible sympatry of individuals. As such, these results run counter to the prediction that *P. leonensis* would be more likely to have less negative stable isotope ratios indicative of open country grazing. In this study, the isotopically most negative individual is *Parahippus* II. Isotope ratio means for *Parahippus* I of -10.5‰ δ^{13}C and -0.11‰ δ^{18}O are actually quite close to the combined *Archaeohippus* I and II means of –10.7‰ δ^{13}C and –0.4‰ δ^{18}O for both carbon and oxygen. If the isotopic ratios of *Parahippus* II indicate resource partitioning or displacement, it is toward even more shaded areas than those exploited by *A. blackbergi.* Although no postcranials were associated with any of the specimens used in this study, the teeth of both *Parahippus* I and II are similar in size

(*Parahippus* I p4 apl=14.7mm, mlw=12mm and m2 apl=14.7mm, mlw=10.6mm; *Parahippus* II p4 apl=15.1mm, mlw=14.0mm and m2 apl=14.2mm, mlw=10.2mm). Therefore, it is not possible to determine whether *Parahippus* II was an especially large individual, or a juvenile male relegated to a marginal habitat as has been speculated for individuals in the population of *A. blackbergi* from Thomas Farm (Chapter 3). Interestingly, the δ^{18}O curve for *Parahippus* II (Fig. 15b) shows that this individual required by far the greatest amount of time to erupt its dentition, suggesting that *Parahippus* II indeed was a large male.

A consistent difference of birth season can be seen in the plots of δ^{18}O. The four Florida specimens exhibit a Fall/Winter birth pattern, with the initial tooth positions mineralized during the season of low δ^{18}O. The two specimens from Wyoming exhibit a spring/summer pattern, the initial mineralizations occurring during a period of enriched δ^{18}O. In instances of seasonal births, births are timed to coincide with peak primary productivity. This further emphasizes the distinct nature of these two environments. In Florida during the early Miocene, winter births probably provided the advantage of avoiding the summer forest fire season. Summer births in Wyoming provided foals with enough time to feed on deciduous forbs before being forced to rely on evergreen forbs and trees. This would explain the increase in δ^{13}C that corresponds with the Winter decrease in δ^{18}O (Fig. 18a, b).

Conclusions

The stable oxygen isotope results of this study contradict the hypothesis proposed in the Introduction that body size reduction in *A. blackbergi* relative to the larger, more primitive equid *M. obliquidens* was the result of the evolutionary heterochronic process

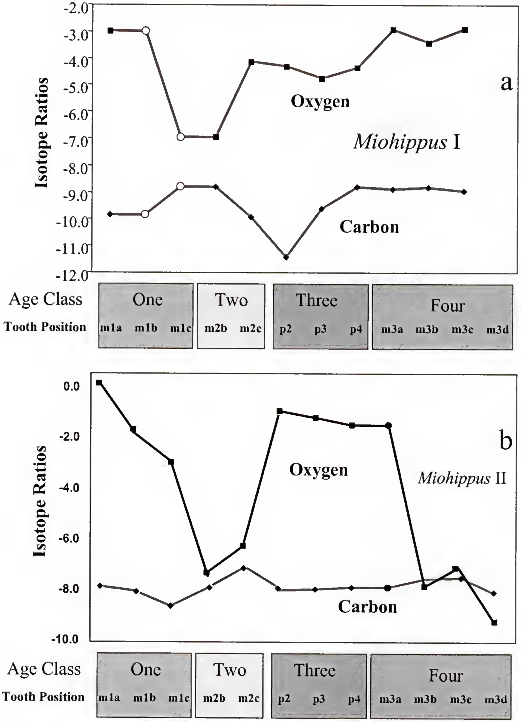


FIGURE 18. Plots of $\delta^{18}O$ and $\delta^{13}C$ for specimens of *Miohippus obliquidens* from the Orellan Goshen Hole Harvard Fossil Reserve of Wyoming. Symbol usage as described in the caption to Fig. 13.

called progenesis. Progenesis involves the reduction of developmental timing in a descendent species relative to that of an ancestral species. The results of this study demonstrate that *A. blackbergi* erupted its adult dentition in 2-2.5 years, whereas *M. obliquidens* erupted its dentition in about 1.5 years. However, an analysis that includes the nearest sister species, either *Parahippus pawniensis* or the common ancestor of *Archaeohippus* and *P. pawniensis*, there will be a chance to better test the idea of ontogenetic reduction to achieve body size reduction. Ontogenetic timing of pony breeds falls within the very broad range found in *E. caballus*. In fact, the smallest breed of *E. caballus*, the Falabella miniature horse, has an extended gestation of nearly 13 months (Greenwood Studs, 2001; Horses Canada, 1999). The hypothesized cause of body size reduction in *Archaeohippus*—progenesis—has no precedent in either naturally or artificially dwarfed *Equus*.

There is no strong evidence of dietary differentiation between *A. blackbergi* and *P. leonensis*. There is, however, a suggestion of differences with the diet of *M. obliquidens*. However, this difference may be due to environmentally induced differences in photosynthetic activity, in local flora between the two environments, or in habitat structure (closed vs open). The dietary carbon intake of the Florida taxa shows seasonal variation in $\delta^{13}C$ that corresponds with seasonal variation in $\delta^{18}O$. This indicates that cyclic variation in photoperiod and water availability results in predictable cyclic variation in photosynthetic activity, and thus variation in carbon discrimination. The pattern of $\delta^{13}C$ cyclicity is the reverse of $\delta^{18}O$ cyclicity for *Miohippus* I and II. This suggests a seasonal dietary shift from deciduous forbs in the summer to evergreen forbs and trees in the winter in a high latitude ecosystem.

This study provides confirmation of ontogenetic timing in Oligocene and Miocene equids as discerned from a study of tooth eruption and wear rates (Chapter 3). It adds to that study information regarding seasonality of reproduction and diet in equids, and the profound influence of ecosystems on such fundamental aspects of life history and ecology.

CHAPTER 5
CLADISTIC ANALYSIS OF ANCHITHERE HORSES

Introduction

Cope (1886) described a partial skull with dentition from Cottonwood Creek, Oregon as *Anchitherium ultimum*. He stated that this was a small animal with a dental series about the size of *Miohippus longicristis*, rugose enamel, and 1) well marked external cingulum on premolars and molars, 2) internal cingulum on P2 and weak ones around protolophs of M23, 3) protoconule that forms an angulation in the premolars and a rounded enlargement in the molars, 4) triangular hypostyle, assymetrical arrangement of incisors and lack of left canine [probably pathological or preservational artifacts], 5) cupped I3 crown, 6) long diastema, 7) dP1 single rooted and small, 8) profoundly large and deep preorbital fossa separated from anterior orbit by a vertical bow, 9) anterior orbit above anterior M3, 10) infraorbital foramen above middle of P4, 11) narial notch extends over 40% of the diastema, 12) palate extends anteriorly as far as posterior border of dP1.

Gidley (1906), after examining additional material from the same locality, assigned this taxon to his new genus *Archaeohippus*. He disputed Cope's (1886) description of 4) the dP1 as small and single rooted, stating that its greatest diameter is 10mm and that it is double rooted, and added that the dp1 also is double-rooted. He added 9) metaloph connected to ectoloph, 10) large protoconule, 11) deep notch in the external protoloph wall between protoconule and protocone with a more shallow notch on the internal wall, 12) little to no crochet, 13) premolars series nearly equal to (but not larger than) molar series, 14) well developed internal cingulum on upper and lower cheekteeth. He had never seen the internal cingulum in any other horse, only in *Paleotherium*.

To the generic description, Osborn (1918) added 1) sharply crested cones and conules that are purely lophoid, not bunoid, 2) internal cingulum vestigial or wanting (contra Gidley, 1906), 3) hypostyle undeveloped, 4) M3/m3 unreduced, 5) incisors small.

Merriam (1913) described *Parahippus mourningi* from the late Barstovian of the Mohave Desert. The available material included a maxilla fragment with dP34 and M1, and a mandible fragment with p3-m2. He considered it distinct from *Archaeohippus* due to 1) absence of a cingulum around the protoloph, 2) higher cusps, 3) very large protoconule, 4) triangular hypostyle, 5) less developed crochet. In Merriam's (1913) view, assignment of this youngest species to *Archaeohippus* would involve reversal in the development of the crochet from the condition in *A. ultimus*. Osborn (1918) placed *P. mourningi* in *Archaeohippus* with no comment on this apparent reversal.

Archaeohippus penultimus was described by Matthew (1924) from a fragment of lower jaw with p3-m1 from the late Hemingfordian - early Barstovian Sheep Creek beds of the Stonehouse Draw Quarry of Nebraska. The author considered it distinct from *A. ultimus* based on the smooth enamel and lack of metastylid of an m3 from the Pawnee Creek beds that was referred to this taxon. Matthew (1932) briefly described juvenile specimens of this taxon, and discussed the phylogenetic position of the genus. He placed it within *Parahippus* based on its possession of 1) rugose enamel, 2) perforated protoloph, 3) partially separated protocone, 4) rounded and separated metaconid/metastylid, 5) unreduced M3/m3, and 6) preorbital fossa like that of *P. pristinus*. He considered it distinct in the lack of a crochet.

Interestingly, none of the above authors commented on the closure of the postfossette by the hypostyle. This relatively advanced character occurs in at least some teeth in specimens of these species. In Hay's (1924) study of the Garvin Gully Local Fauna, the author made note of this condition in the two small horses he named from there. Hay's description of *Miohippus blackbergi* includes these characters: 1) ectoloph and protoloph form an angle of approximately 75 degrees, 2) parastyle and mesostyle prominent, 3) ribs well developed, 4) protoloph interrupted by protoconule, 5) no break between metaconule and hypocone, 6) metaloph connects to lamina from ectoloph, but connection is deeply notched, 7) protoloph also notched [perforated], 8) triangular hypostyle not wholly free from posterior cingulum, 9) triangular hypostyle joins the metaloph and ectoloph to close the postfossette, 10) no crochet, 11) anterior and posterior upper cingula present, 12) labial and lingual upper cingula are weak, 13) p34 slightly wider than m12, 14) lower lingual and labial cingula present, 15) minute tubercle in ectoflexid, 16) some cement on labial cingulum, 17) no metaconid-metastylid twinning or sometimes a faint development in deciduous teeth 18) deciduous metaconule stronger than that seen in permanent cheekteeth, 19) molars more lophodont than premolars.

Hay (1924) described *Parahippus minutalis* as possessing: 1) protoloph and metaloph fully connected to ectoloph, 2) protoconule separated from protocone by slight constriction, 3) metaconule separated from hypocone by a similarly slight constriction, 4) triangular hypostyle rests on posterior cingulum, 5) hypostyle joins metaloph and ectoloph to close postfossette, 6) crochet present, 7) crochet presses against, but not merged with, protoloph, 8) no additional plications in the fossettes, 9) styles are prominent, 10) ribs are low and rounded 11) labial, anterior, and posterior cingula are strong, 12) lingual cingulum weak, 13) no cement, 14) anteroposterior length about 0.55 the mediolateral width.

These two taxa were distinguished by 1) swollen protoconule (*M. blackbergi*) vs. slight constriction of protoconule from protocone (*P. minutalis*) [however, Forsten (1975) saw the latter in only one specimen from Garvin Gully, and this constriction was included in the diagnosis of *Archaeohippus* by Gidley (1906)], 2) metaconule indistinct (*M. blackbergi*) vs. constricted from hypocone (*P. minutalis*) [in general, the metaconule is not well developed in *Archaeohippus*, and this character varies between these two states within a population], 3) crochet absent (*M. blackbergi*) vs. present (*P. minutalis*), 4) labial cingulum weak (*M. blackbergi*) vs. strong (*P. minutalis*), 5) some cement (M. *blackbergi*) vs. none (*P. minutalis*).

The crochet is the crux of any argument for the separation of the sample of small horses from Garvin Gully into two taxa, for, by original definition, *Archaeohippus* completely lacks the crochet. However, Forsten (1975) asserted that all of Hay's (1924) diagnostic characters were variable within populations of *A. blackbergi*. Forsten saw the crochet more frequently in the dP's and M3 than in P2-M2. While Hay saw no additional plications in Garvin Gully animals at the time of his study, Forsten saw one on an M3 posterior metaloph. Additional plications are common and variable features in the Thomas Farm sample. For instance, specimen UF 156481 has crochets on R P2, M1-3, L P2, P4, M1-3; prefossette plis on R M1; postfossette plis on R+L M1 and M2). In addition, Forsten (1975) saw crochets connected to the protoloph on 3 dPs. This advanced character did not appear on any of the 150 permanent Ps she saw. However, it is not uncommon in the Thomas Farm sample available to the present writer. The lingual cingulum is also common in the Thomas Farm sample, although it is rarely complete or strong.

Bode's (1933) study of the dentition of *Archaeohippus mourningi* from the North Coalinga Local Fauna of the Temblor Formation revealed 1) a triangular hypostyle that encloses a small fossette, 2) reduced M3, 3) broad protocone and hypocone that obstruct the medivallum, 4) less distinct paracone rib, 5) very weak to absent labial cingulum, 6) higher crowned (than *A. ultimus*), 7) no cement, 8) no crochet.

In contrast, Bode (1933) considered *Archaeohippus ultimus* from the Mascall of Oregon to be more primitive because its teeth show 1) hypostyle not triangular, just a built-up cingulum, 2) unreduced M3, 3) narrow protocone and hypocone that do not close off medivallum, 4) middle external rib on paracone wall is more distinct (like *A. mourningi* dP3 but not adult teeth), 5) heavy internal cingulum (especially on protocone of M2 and M3), 6) crown height like advanced *Miohippus*, 7) lower cheek teeth are similar to *A. mourningi*, though lower crowned and slightly smaller.

Bode (1933) considered *Archaeohippus penultimus* to be very similar to Coalinga *A. mourningi* except for 1) weaker parastyle and mesostyle than in Coalinga specimens, 2) stronger median external rib of paracone, 3) wider valley between protoloph and metaloph, 4) lowers have slightly less separate metastylid-metaconid columns.

Archaeohippus penultimus also displays 1) faint labial cingulum on paracone and metacone interrupted by the mesostyle, 2) internal cingulum present on dP2 only, which has a parastyle larger than its conical paracone, 3) all paracones have some development of a median rib, 4) triangular hypostyle with fossette, 5) unperforated rectilinear protoloph with 6) constriction between protoconule and protocone, 7) thin metaloph with indistinguishable metaconule. Lowers of AMNH 21532 show 1) as is typical of the deciduous lower cheekteeth of all species of *Archaeohippus*, greater metaconid-metastylid twinning than seen in the permanent cheekteeth, 2) cingulum present on anterior and external sides of the protoconid, 3) milk teeth have a ledge between the protoconid and hypoconid, 4) external cingulum only on hypoconid of dp2.

Bode (1933; p. 53) went on to describe the configuration of the trigonid of the dp2 of AMNH 21532, with its "paraconid and protoconid of equal size…[t]he paraconid is situated in front of and only slightly interior to the antero-external cusp. The metaconid is placed almost directly inside the protoconid, so that the anterior loph in this tooth forms almost a right angle. The valley between the protoconid and hypoconid slopes downward and to the rear, while its position is almost vertical in the deciduous teeth posterior to the second." This he contrasts with the p2 of an adult specimen of *A. mourningi* (AMNH 12244) with its "paraconid…placed anteriorly to the metaconid rather than the protoconid as in dp2 of *A. penultimus*. The protoconid-hypoconid valley has the primitive backward slope."

White (1942) decided that isolated teeth lacking a connection between the metaloph and ectoloph in some Thomas Farm specimens represented a rare species of *Miohippus*. A study of complete dentitions reveals that this character state is variably present within individuals, and is particularly common in deciduous teeth.

Downs (1956) reported similarity in size and morphology between *A. ultimus* and *A. blackbergi*, with *A. mourningi* larger and morphologically distinct from these two; *A. penultimus* was considered a likely chronospecies with no distinction from *A. blackbergi*.

Forsten (1973) asserted that *Archaeohippus* is removed from ancestry of *P. leonensis* because of reduction of M3m3; in particular, she interprets differential ontogenetic trajectories in the growth of the third molars relative to the second molars. However, no reduction was observed in the later species as described above; Osborn (1918) and Gidley (1906) saw no reduction in M3 in *A. ultimus* and Matthew (1932) saw none in *A. penultimus*. Bode (1933) did describe reduced M3 in *A. mourningi*. Forsten's (1973) analysis of tooth size and evolution in equids assumes a baseline condition in *M. bairdi*. Relative to this condition, the tendency to reduce the M3/m3 was seen in *A. blackbergi*, *P. leonensis*, *Anchitherium*, and *Hypohippus*, but not in *P. nebrascensis*. Thus, reduction of M3 was a common trend among anchitheres and parahippines. Ontogenetic trajectories can differentiate taxa, but are reversible and thus not exclusionary characters.

A stronger trend in *Archaeohippus* is the elongation of p2/P2, which is an equine character. In the same study (Forsten, 1973), P2 length is seen to be relatively greater in *A. blackbergi*, *P. leonensis*, and *P. nebrascensis*, but not in *Anchitherium*, *Hypohippus*, or *Megahippus*, while the p2 is elongated in *A. blackbergi*, *P. leonensis*, *Anchitherium*, and *P. nebrascensis*, but not *Hypohippus* and *Megahippus*.

Unfortunately for this present study, Forsten (1973) lumped disparate samples together in her analysis. Of particular relevance is the fact that *Mesohippus bairdi* and "*Miohippus antiquus*" (=*Mesohippus barbouri* and *Miohippus obliquidens* [Prothero and

Shubin, 1989]) are both represented on plots by the letter M by Forsten (1973). Thus, the distinctions between these genera, already partially blurred by the use of the Harvard Fossil Reserve material grouped under the name "*M. antiquus*," are unavailable to the reader.

Forsten (1974) acknowledges that the shape of the hypostyle can be very variable within one tooth row, thus, hypostyle shape of isolated teeth is not a strong diagnostic. However, as Downs (1956, p. 255) states, the hypostyle and posterior cingulum closing the postfossette are important diagnostic characters.

Scott (1941) observed that within the Equidae there is an apparent reversal in the evolution of the canine. *Hyracotherium* possessed large, pointed canines. In *Mesohippus*, the upper canine is reduced and the lower incisiform. In later equids, the upper and lower canines are again pointed and project beyond the occlusal plane of the incisors.

Notes on Two Important Taxa

Miohippus obliquidens. Schlaikjer (1935, p. 141) emphasized the importance of the Oligocene Harvard Fossil Reserve in Goshen County, Wyoming because of its large sample of equids from a period which "is probably the most critical in the evolution of the horse, for the direct ancestral forms of at least five important late Oligocene and early Miocene genera were becoming established." He described three equid taxa from this locality. In his study, he considered the development of the crochet to be "the most important single character in dental change during the evolution of the direct progenitors of the horse, particularly in the formative period from Oligocene to Miocene times" (pp. 142-143). Thus, he erected the genus *Pediohippus* to include those Oligocene taxa that possess a crochet without possessing a metaloph-ectoloph connection. In Schlaikjer's (1935) conception, *Pediohippus* evolved into *Parahippus pristinus*, which possessed small crochets and a metaloph-ectoloph connection and was thus the progenitor of all *Parahippus* other species. Scott (1941) agreed with Schlaikjer's phylogenetic hypothesis, and explained that the non-crochet bearing taxa left in *Miohippus* were the progenitors of the Anchitheriinae *sensu stricto*.

Forsten's (1974) study of the Goshen Harvard Fossil Reserve asserts that the equid sample is homogeneous, not composed of *Pediohippus antiquus*, *Miohippus obliquidens*, and *Mesohippus barbouri*, as Schlaikjer (1935) suggested. She rediagnosed all specimens as *Miohippus antiquus* based on the presence of a strong facet for the cuboid on the MT III in most specimens, which she considered a more diagnostic character than the presence or absence of a weak crochet. Prothero and Shubin (1989) stated that *M. antiquus* is a junior synonym of *M. obliquidens*. They also argue that Forsten (1974) failed to recognize the presence of *Mesohippus barbouri* represented by 2 smaller skulls vs. 10 larger *Miohippus* skulls and 2 MT III without a clear cuboid facet vs. 9 with this facet. My own study of this collection at the MCZ revealed 2 right mandibles with very strong cingula and lacking an enlarged m3 in contrast with the other 19 right mandibles. However, the cuboid articulation may not be a definitive diagnostic of the *Mesohippus-Miohippus* distinction either. It seems to develop gradually and variably in parallel lineages.

***Miohippus equinanus*.** The placement of *Miohippus equinanus* has been the focus of a small debate for decades. Osborn's (1918) description of material from late Early Arikareean Porcupine Creek of South Dakota clearly describes a parahippine.

Characters include metalophs connecting to ectolophs in early wear, elongate P2 parastyle, strong metaconid-metastylid twinning, connection of the cristid obliqua to the metastylid in early wear, and progressive foot structure. The final line of the description states that the dentition and foot structure are "…in some respects…so progressive as to present an approximation toward the dental type of *Parahippus*" (p. 66). Regardless of the above, Osborn assigned this species to *Miohippus*. Stirton (1940) left this taxon in *Miohippus* but suggested that it may have been ancestral to *Archaeohippus*. Skinner et al. (1968) placed this species within *Archaeohippus*.

Prothero and Shubin (1989, p. 169) rejected the notion that *M. equinanus* could be ancestral to *Archaeohippus* because it lacks both the high metaloph-ectoloph connection and high, triangular hypostyle of *Archaeohippus*. These authors also were uncertain whether this taxon could be assigned to *Miohippus* because "[n]o skulls or postcrania have been found that could show whether it has the diagnostic features of *Miohippus.*" This statement is true of the Whitneyan material from the Leptauchenia nodules referred to *M. equinanus* by the authors. However, postcranial material was available to Osborn (1918) for his description of the material from the Arikareean, and additional specimens were referred by MacDonald (1963) from the Wounded Knee fauna and Skinner et al. (1968) from the Wewela fauna of the Turtle Butte Formation. Inspection of the Whitneyan material referred to *M. equinanus* by Prothero and Shubin (1989) reveals it to belong to another taxon, probably a late surviving species of *Mesohippus*. Thus, there is no evidence of *M. equinanus* in the Whitneyan.

A. penultimus distal MT III articular width/epicondylar width=13/15.5=0.84, whereas *M. equinanus*=13/16.5=0.79. Thus, *M. equinanus* has the same articular width as *A. penultimus*, but broader, flaring epicondyles like *P. leonensis*.

The type of *Miohippus equinanus* AMNH 12912 is a partial palate with LdP1, P2-M3 (latter is erupting), R dP1, P2-P3; dP1 heavily worn and flattened, yet M3 not fully erupted. Upper cheek teeth have a wear pattern that indicates eruption sequence of dP1, P2, P3, M1, P4, M2, M3 quite unlike the eruption pattern in *Archaeohippus* and *P. leonensis*. AMNH 12912 also has 1) low hypostyle; 2) relatively small protoconule; 3) no connections of metaloph to ectoloph on P2, M23, weak connections on P4; 4) lophs not as steep sided and distinct as in *Archaeohippus*--the lophs grade into the fossettes and medivallum, obscuring these valleys; 5) M3 unreduced; 6) m3 heel is very large, like *Miohippus* (seen on 12916 paired mandibles with R i1 - m3, L i1 - m2); 7) lower canines very incisiform, incisor arcade very procumbent and circular.

M. equinanus has an oblique metapodial head (unlike *Archaeohippus*).

After the above observations were made, a cladistic analysis was performed to test the hypothesis that the species of *Archaeohippus* form a monophyletic clade more closely related to the parahippines than to *Anchitherium* and its kin in the ASS.

Materials and Methods

A matrix of 21 taxa and 62 characters was compiled in MacClade 4.0 and analyzed in PAUP 4.04b4a for MacIntosh. Two programs were used because MacClade is superior for matrix construction, and PAUP is more versatile at matrix analysis. Measurements taken on certain species were combined into a generic category. Thus, *Hypohippus* includes *H. affinis* (characters 1-35), *H. pertinax* (characters 39-54) and *H.* sp (characters 55-62). *Kalibatippus agatensis* was represented only by character 59, and this was inserted into the analysis of *K. praestans*, which lacked that character. *Megahippus mckennai* had only four characters (30-33) coded, and of these, differed from *M. matthewi* in characters 31=1 and 32=0. *Miohippus intermedius* was dropped from the analysis becase it had been coded for characters 56 and 59-62, all of which had character states identical to those of *M. obliquidens*. The resultant matrix was analyzed with two heuristic searches with branch swapping for 1000 replicates, one with an *a priori* assignment of an outgroup, and one without. "Heuristic search" is the term given by PAUP for the initial, basic analysis performed by that application. "Heuristic" means that the procedure addresses all available evidence to "discover" patterns that are used to construct hypotheses (phylogenies) that can be tested by other means. A bootstrap analysis with 1000 replicates was also performed. This is a matrix analysis procedure that constructs new matrices from the original. The result is a tree with numbers at each node that represent the percent retrieval of that node in the numerous trees that were constructed from the 1000 iterations of the matrix rearrangement procedure. Strict consensus trees were created that present only those clades that are found in every one of the trees from the heuristic analyses. Majority-rule consensus trees were constructed to show percent retrieval of all clades with >50% occurrence in the heuristic analyses. For each heuristic analysis, two indices were calculated. One is the consistency index (CI), which compares the minimum possible number of steps (m) a character requires to proceed through its transformation series with the observed number of steps (s) for a particular tree (CI = m/s). (A binary character changes from 0 to 1 once, so m = 1; for a unidirectional three state character m = 2, etc.). The retention index (RI) calculates the amount of apparent synapomorphy versus actual synapomorphy by comparing m and s against the maximum number of steps (g) possible for a transformation series (RI = g-m/g-s) (Wiley et al., 1991).

Characters Used in this Analysis

1. Relative length of face: if the orbit+cranium>1.1 times the length of the face=0; orbit+cranium≤1.1 times the length of the face=1.
2. Placement of anterior edge of the orbit: over anterior M2=0, over posterior M2=1, over anterior M3=2.
3. Zygomatic notch: if the posterior surface of the maxillary component of the zygomatic arch is beside M3 code=0; behind M3 code =1.
4. Lacrimal facial fossa: none=0, shallow=1, deep=2.
5. Malar facial fossa: none=0, shallow=1, deep=2.
6. Malar facial fossa pocket: none=0, small=1, deep=2.
7. Diastema: I3-P2 length/M1-3 length<1 code=0; ≥1 code=1
8. Precanine Diastema Length: precanine diastema length/postcanine diastema length <0.3 code=0, ≥0.3 code=1.
9. Premolar eruption: P2-P4 eruption sequential=0; P2-P4 nearly simultaneous=1
10. Ribs on ectoloph (these are the labial surface of the paracone and metacone): strong=0, weak=1, none=2.
11. Upper molar shape: oblique=0, square=1.
12. Protoloph connection to ectoloph: usually low=0, usually high=1.
13. Metaloph connection to ectoloph: none=0, low=1, high=2.

14. Metastyle development vs. mesostyle development: weak=0, subequal=1, strong=2.

15. Protocone shape: round and positioned lingual to paracone=0; elongate and positioned posterior to paracone=1; low and conical with most of the cone directed labially toward paracone=2; low and lingual as in 2, but with extensive development in the lingual direction also.

16. Protoconule vs. protocone: no protoconule=0, protoconule smaller=1, protoconule larger than protocone=2

17. M1 hypocone apl vs. protocone apl: protocone larger=0, hypocone larger=1, hypocone and protocone equal=2.

18. M1 hypocone mlw vs. protocone mlw: protocone larger=0, hypocone larger=1, hypocone and protocone equal=2.

19. Protoconule vs. protoloph: protoconule distinct=0, protoconule submerged in protoloph=1.

20. Metaconule vs. hypocone: no metaconule=0, metaconule smaller than hypocone=1, metaconule larger than hypocone=2.

21. Metaconule vs. metaloph: metaconule distinct=0, metaconule submerged in metaloph=1.

22. Hypostyle height: low=0; high=1.

23. Hypostyle part A (see diagram): not connected to metaloph=0, connected to metaloph=1.

24. Hypostyle part B (see diagram): not connected to ectoloph=0, connected to ectoloph=1.

25. Hypostyle part C (see diagram): weak with little lingual extension=0, strong with large lingual crista=1.

26. Medivallum between protocone and hypocone: open=0, closed by the swollen bases of the protocone and hypocone=1.

27. Crochet: none=0, small=1, medium=2, large and connected to protoloph=3.

28. Additional plications: none=0, few=1, many=2.

29. Upper lingual cingulum on premolars: present=0, weak=1, absent=2

30. Upper lingual cingulum on molars: present=0, weak=1, absent=2.

31. Relative size of dP1: large=0, small=1.

32. P2 elongation (apl/mlw): index<1 code=0, index ≥1 code=1.

33. P2 anterostyle: absent=0; present=1.

34. M3 hypocone reduction (anterior mlw/posterior mlw): index<1.1, code=0; index≥1.1 code=1.

35. Space beside primary cones: none=0, a little=1, lots of space around columnar cones=2.

36. P2-4 apl vs. M1-3 apl: PM≤M=0, PM>M=1.

37. Lower canine morphology: caniniform=0, incisiform=1.

38. Lower cheek tooth profile: labial and lingual sides approximately equal in height=0; labial side deeper=1.

39. Lower labial cingulum on premolars: present=0, weak=1, absent=2.

40. Lower labial cingulum on molars: present=0, weak=1, absent=2.

41. Lower lingual cingulum on premolars: present=0, weak=1, absent=2.

42. Lower lingual cingulum on molars: present=0, weak=1, absent=2.

43. Cristid obliqua: retracted from metastylid, very low connection=0; low connection, not retracted=1; high connection=2.

44. Orientation of p2 protoloph rib: posteromesial=0, mesial=1.

45. Metaconid/metastylid twinning on p2: absent=0, present=1.

46. Metaconid/metastylid twinning on p3-m3: none=0, weak=1, strong=2.

47. Timing of connection of cristid obliqua to metastylid on m2 versus wear on m3 heel: heel wear present=0; heel wear absent=1.

48. Timing of connection of cristid obliqua to metastylid on m3 versus wear on m3 heel: heavy wear=0; light wear=1.

49. Relative size/morphology of m3 heel: large with basin (fossetid)=0; small with small basin=1; small with no basin=2.

50. Development of p2 paraconid: small=0; large=1

51. Elongation of p2 (p2 apl/p2-p4 apl): index>3.00 code=0; index≤3.00 code=1.

52. Reduction of m3 (apl/mlw): index<2.50 code=0; index≥2.50 code=1.

53. Posterior p4 mlw vs. anterior m1 mlw: p4≤m1=0; p4>m1=1.

54. Posterior p3 mlw vs. anterior m1 mlw: p3≤m1=0, p3>m1=1.

55. MC III unciform facets: vertical and separate=0, oblique and separate=1, oblique and merged=2.

56. MT III midshaft cross section: flat oval=0, round oval=1.

57. MT III cuboid facet: absent=0, weak=1, strong=2.

58. MT III mesoentocuneiform facet: absent=0, present=1.

59. Lateral metapodials: robust=0, ml narrow=1, ap narrow=2.

60. Proximal phalanx III V-scar: none, component scars still distinct from each other=0; short=1; long (greater than 1/4 phalanx length)=2.

61. Proximal phalanx III length vs. proximal width index (length/proximal mlw): index<1.5 code=0; index≥1.5 code=1.

62. Proximal phalanx III length vs. midshaft width index (length/midshaft mlw): index<2.0 code=0; index≥2.0 code=1.

Taxa Used in this Analysis

Anchippus texanus AMNH 10764 and Toledo Bend specimens (from Albright 1999); *Anchitherium clarencei* MCZ 19930, UF/FGS V-5243, MCZ 7608 UF 175395; *Anchitherium gobiense* AMNH 26501; *Archaeohippus blackbergi* Thomas Farm composite including skull UF 165880; *Archaeohippus mannulus* UF 160784; *Archaeohippus mourningi* AMNH 111743, UCMP 19840; *Archaeohippus penultimus* FAM 71650, AMNH 21535, AMNH 18950; *Archaeohippus ultimus* AMNH 8174; *Desmatippus crenidens* AMNH 10782 (cast of PU 10430); *Desmatippus integer* AMNH 81094, ANMH 17567, AMNH 17568; *Hypohippus affinis* FAM 107596, AMNH 10771 (cast of USNM 573); *Hypohippus pertinax* AMNH 17232; *Hypohippus sp.* FAM 60628, FAM 60627; *Kalibatippus agatensis* AMNH 14211; *Kalibatippus praestans* AMNH 7269; *Megahippus matthewi* ; *Mesohippus bairdi* AMNH 6841(cast of USNM 8632); *Mesohippus stenolophus* NMC 6302, NMC 6303; *Miohippus annectens* YPM 12230, AMNH 11275; *Miohippus equinanus* AMNH 12912, AMNH 12916; *Miohippus obliquidens* Harvard Fossil Reserve composite including MCZ 2790 and UF specimens; *Parahippus leonensis* Thomas Farm composite, UF specimens; *Parahippus pawniensis*

AMNH 9085, AMNH 107838 (cast of USNM 42499), AMNH 71705 AMNH 109858; *Parahippus tyleri* AC 4522 (cast).

Table 8. Taxon/Character State Matrix used in the PAUP analyses.

Anchippus texanus	?????????01011010?01000000201 1?????????0?02??????????????????11
Anchitherium clarencei	0011001111102120001010111000010111 11?1001111010021 1100?021?000
Anchitherium gobiense	??1??????210?0202?1010000100001101?1??????????????????????????
Archaeohippus blackbergi	01?2211?10101201220101111111120111210111121011101110011202111
Archaeohippus mannulus	??1?????1010110122010111011111111?2?0100112101111111111?02111
Archaeohippus mourningi	12?2211???1022012?0111111100010??120?111112101110?1?11?120?111
Archaeohippus penultimus	0012211??01012022?010111101?0101112101001121011111110011202111
Archaeohippus ultimus	?2122110??1?1?010????111111101011120?111112101?????????120?111
Desmatippus crenidens	?????????1101?11??010111002?22011?1??1121121?1112111??????????
Desmatippus integer	?????????11021010200111111211201 1?1??1012221?2?1?11?11????????
Hypohippus	10020001?2101100001010011000111 1001???00222101012101002 1?11000
Kalibatippus praestans	?2110001110011310200101000002210001 10?00221??100111000??211?00
Megahippus matthewi	?????????20010300?1010000000001?10?1????????????????????????????
Mesohippus bairdi	000100000000021220100000000000?0001?0100011000100000100001 00000
Mesohippus stenolophus	?????????1001121220100010000 00???11??100??2001??0?????????????
Miohippus annectens	111100111000023 10?0100001000220001 01??????????????????????????
Miohippus equinanus	????????0010112102010010100011110111111111100100001 0??????????
Miohippus obliquidens	????????1000013100000001000022010110?10111000000000000000201000
Parahippus leonensis	12110001101022111101011100322201112101222221121121111111202111
Parahippus pawniensis	?1120001111012012201011111211101 1?21?1001121011111100?1??2?11
Parahippus tyleri	011100011111221 12?0101110030110111?101002221?11101111?????????

Results

The results of the analysis are presented as phylograms with branch lengths indicated numerically and graphically (Figs. 19-27). The heuristic analysis with *M. bairdi* as outgroup produced 106 shortest trees 190 steps long, C.I.=0.45 and R.I.=0.59. Figure 19 is an example of the dominant pattern seen in 95 trees. It includes a monophyletic *Archaeohippus*. *A. mourningi* and *A. ultimus* consistently form a small clade that is often joined with *A. blackbergi*. *A. mannulus* and *A. penultimus* often form a clade. The sister taxon to the entire *Archaeohippus* clade is *P. pawniensis*.

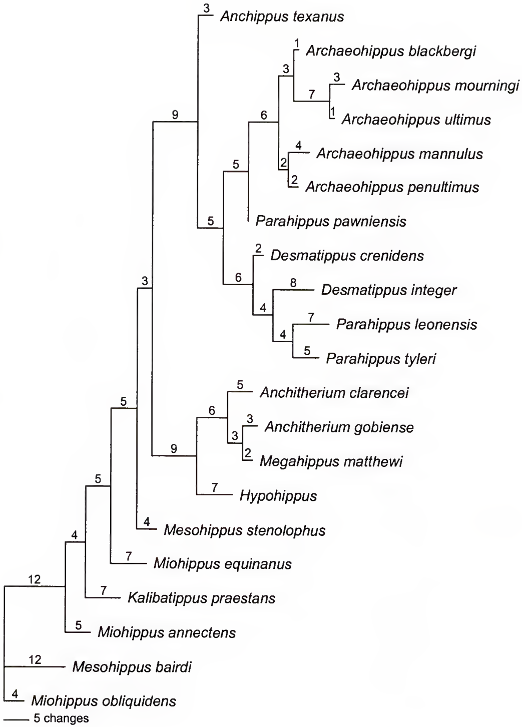


FIGURE 19. Phylogenetic tree of anchithere relationships. This heuristic analysis included the a priori assignment of *M. bairdi* to the position of outgroup. Branch lengths indicate number of changes, also indicated by numbers above branches.

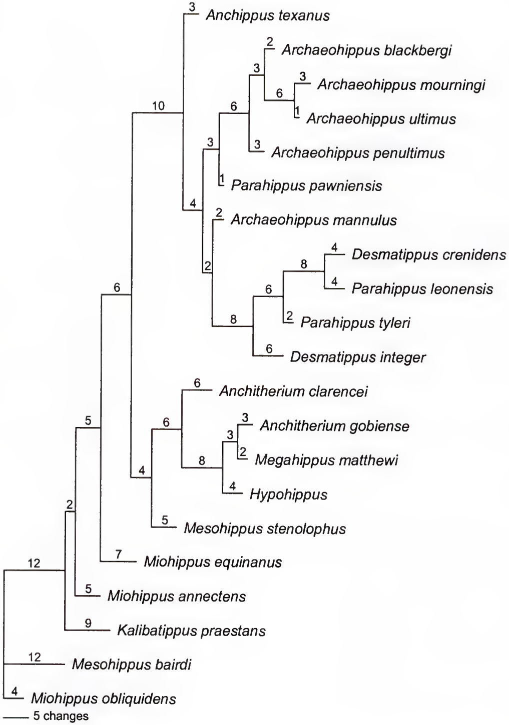


FIGURE 20. Phylogenetic tree of anchithere relationships. This heuristic analysis included the a priori assignment of *M. bairdi* to the position of outgroup. Branch lengths indicate number of changes, also indicated by numbers above branches. Note that this tree differs from the tree in Fig. 19 in that *Archaeohippus* is not monophyletic.

Figure 20 is an example of the secondary arrangement seen in 11 trees, in which the clade is broken by the insertion of *P. pawniensis*. *A. mannulus*, the oldest member of the clade, becomes the sister taxon of the *Desmatippus/Parahippus* clade. Another novel arrangement in Fig. 20 is the pairing of *P. leonensis* with *D. crenidens*. In both Figs. 19 and 20, the sister taxon to both the *Archaeohippus/P. pawniensis* clade and the *Desmatippus/Parahippus* clade is *Anchippus texanus*.

In both Figs. 19 and 20, the above clade is paired with a clade of anchitheres sensu stricto minus *Kalibatippus praestans*, and sometimes including *M. stenolophus*. *K. praestans* is never nested within the ASS.

Interestingly, when the a priori assignment of *M. bairdi* to outgroup status is removed, the topology of the outgroup clades changes considerably (Fig. 21). This analysis also yielded 106 shortest trees of 190 steps with C.I.=0.45 and R.I.=0.59. *M. bairdi*, along with *M. obliquidens* and *M. annectens* move from the outside of the outgroup to one of the crown-most positions in the entire topology. The rest of the non-ASS equids of the outgroup (*M. equinanus*, *K. praestans*, and *M. stenolophus*) join these three taxa to form the sister clade of the ASS. These two clades join to form a trichotomous arrangement with the combined ingroup clade and *A. texanus*. A bootstrap analysis with 1000 replicates and no assigned outgroup produced a tree with three defined clades (Fig. 22). It retrieves the *Archaeohippus/Desmatippus/Parahippus* clade in 74% of the analyses. Within that clade is the *A. mourningi+A. ultimus* clade (69%). It also retrieves the *M. bairdi+M. annectens+M. obliquidens* clade in 54% of the analyses. All other taxa are placed in a basal polytomy.

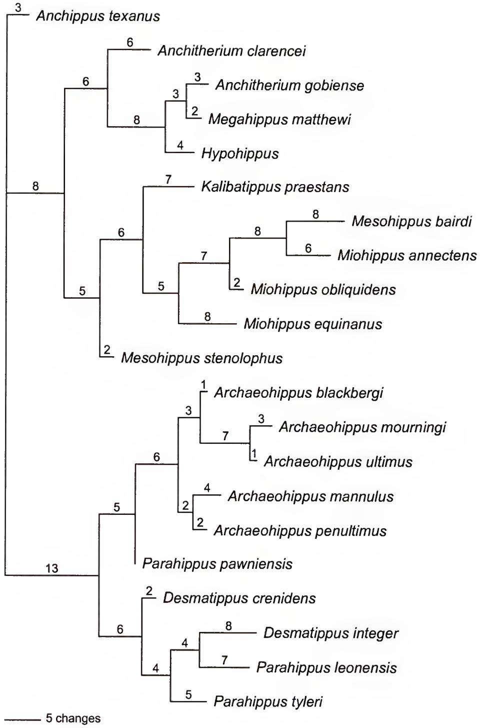


FIGURE 21. This heuristic analysis does not include the a priori assignment of *M. bairdi* to the position of outgroup. Note the placement of *A. texanus*.

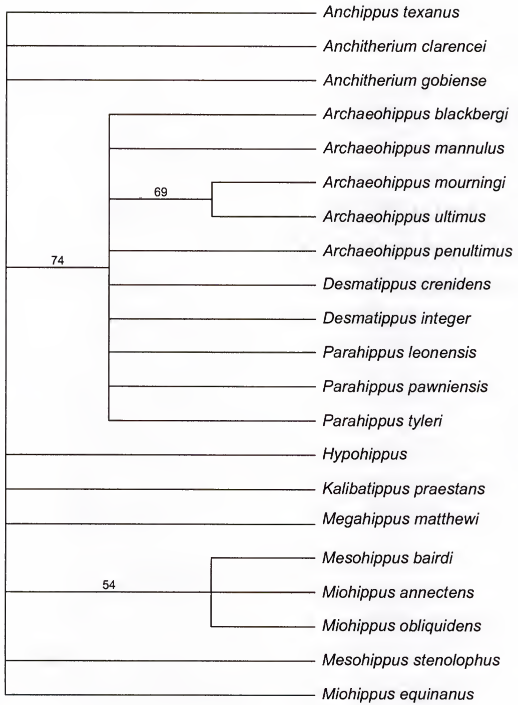


FIGURE 22. Bootstrap analysis of anchitheres without an a priori assignment of an outgroup. Percentages of clade retrieval are indicated above branches. Percentages below 50 are not reported.

Two consensus trees were created for each of the heuristic analyses. For the analysis that includes the a priori assignment of *M. bairdi* as outgroup there is a strict consensus tree (Fig. 23), and a 50% majority-rule consensus tree (Fig. 24). The topology of Fig. 23 is similar to that of the trees upon which it is based except that the *M. bairdi-M. annectens-M. obliquidens* clade is not retrieved and these taxa are placed in a basal polytomy. The majority-rule tree (Fig. 24) resembles the heuristic analysis in Fig. 19 in most details. The second strict consensus tree (Fig. 25) is derived from the analysis with no assigned outgroup. As in Fig. 21, a polytomy exists with one clade composed of *Archaeohippus*, *Desmatippus*, and *Parahippus*, a second clade composed of the mesohippines, miohippines, *K. praestans*, and the ASS, and the solitary taxon *A. texanus*. Within the first clade we see the *A. blackbergi-A. mourningi-A. ultimus* clade supported, as well as the clade composed of *D. crenidens-D. integer-P. leonensis-P. tyleri*. The three most primitive members of this clade – *A. mannulus*, *A. penultimus*, and *P. pawniensis* – form a polytomy with these two clades. In the other major clade, only the ASS clade – *A. clarencei*, *A. gobiense*, *M. matthewi*, and *Hypohippus* -- is supported. The majority-rule tree without an outgroup (Fig. 26) links the outgroup to the ASS clade as in Fig. 21. Otherwise, it does not differ from the majority-rule tree in Fig. 24. All percentages of node retrieval are identical between these two topologies. The retrieval rates of the *Archaeohippus* clade, the *Desmatippus*/*Parahippus* clade, the *Archaeohippus*+*Desmatippus*/*Parahippus* clade, and the ASS clade are all above 90%, with several at 100%.

An additional heuristic analysis without outgroup designation but with weighting of characters according to the C.I. of each character yielded a cladogram (Fig. 27) that is

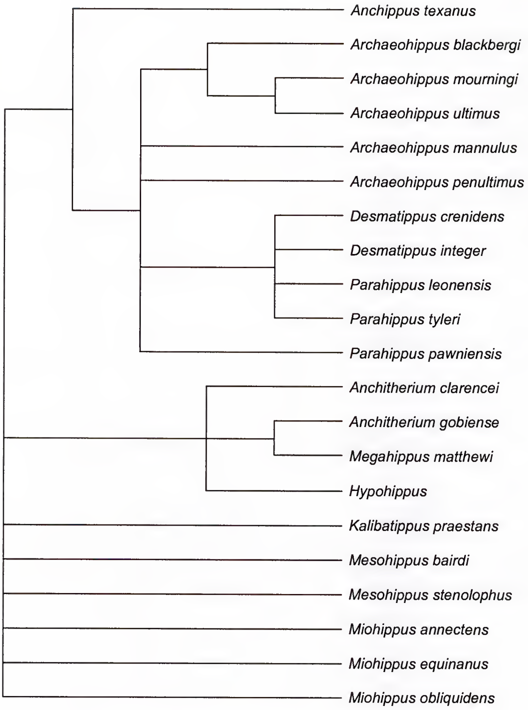


FIGURE 23. Strict consensus tree of anchithere equids with *M. bairdi* as outgroup.

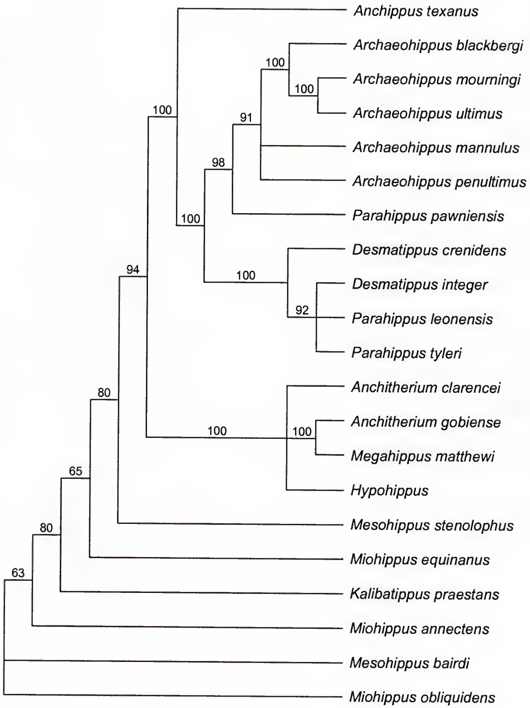


FIGURE 24. Majority-rule tree of anchithere equids with *M. bairdi* as outgroup. Numbers indicate percent of retrieval of topology at each node.

very similar to Fig. 21, the unweighted heuristic analysis with the same analytical parameters. As a consequence of the weighting by C.I., the one shortest tree has a length of 27.9, C.I.=0.71, and R.I.-0.84. Figure 27 differs from Fig. 21 in that *A. clarencei* is removed from the ASS clade and placed at a node immediately basal to *K. praestans*, a move which pushes *M. stenolophus* into the most basal position in the overall clade. *A. mannulus* is moved to a node basal to the other archaeohippines, *P. pawniensis*, and the *P. leonensis*+*P. tyleri* clade. The most removed position in this clade is occupied by the *D. crenidens*+*D. integer* clade. *S. texanus* remains outside both these larger clades.

Discussion

The overall pattern of the above analyses is consistent, particularly when the bias of a preconceived outgroup is removed. Although *M. bairdi*, the type species of *Mesohippus*, is ostensibly one of the most primitive taxa in this analysis, in some regards it is actually very derived for a species of *Mesohippus*. Some specimens possess connected metalophs, others have a strong contact between the cuboid and MT III. This widespread, successful species was evidently experimenting with a range of characters generally associated with miohippines (cuboid facet on MT III) and even more derived equids (connected metaloph). This fact brings with it several implications: either *M. bairdi* is the sister taxon of all the more derived equids, or it is one of these derived equids (not a mesohippine), or the phylogenetic signal provided by these characters is of questionable integrity. Perhaps a more comprehensive analysis including more mesohippines would pull *M. bairdi* out of the clade of fairly advanced miohippines in which it is nested in the results of this study.

The unique position occupied by *A. texanus* almost requires that its generic distinction be maintained for now. Some consider *Anchippus* and *Desmatippus* to be interchangeable names for primitive parahippines. Albright (1999) chooses to use it in place of *Desmatippus* because *Anchippus* has priority. MacFadden (1998) selected *Desmatippus* because the type material is more extensive, permitted better characterization of the genus than is possible with the type material of *Anchippus* (a single, broken upper molar). The results of this study indicate that, given the additional material from Toledo Bend, Texas, assigned to *A. texanus* by Albright (1999), these taxa may actually be distinct. Alternatively, this distinction could be an artifact of too much missing data for *A. texanus* in the analysis. The addition of key character states to the matrix might better resolve this equid's position. Based on the derived phalanges of this taxon, it would almost certainly belong to the *Archaeohippus/Desmatippus/Parahippus* clade, albeit as that clade's most primitive member. It requires two additional steps to place *A. texanus* inside the *Desmatippus/Parahippus* clade, two steps to place *A. texanus* inside the *Archaeohippus* clade, two steps to nest *A. texanus* within the outgroup clade, and 3 steps to place *A. texanus* inside the ASS clade.

Perhaps the most surprising feature of the general topology of these trees is the removal of *K. praestans* from the ASS. Some students have considered *Anchitherium clarencei* to be a species of *Kalibatippus*, a view refuted by MacFadden (2001). An association between these two taxa appears only in the CI weighted heuristic analysis (Fig. 27). In all other analyses, it is constrained from associating with the ASS by the intervention of *M. stenolophus*. Placement of *K. praestans* in the ASS requires a tree two steps longer than the shortest. In the CI weighted analysis, *M. stenolophus* is removed to

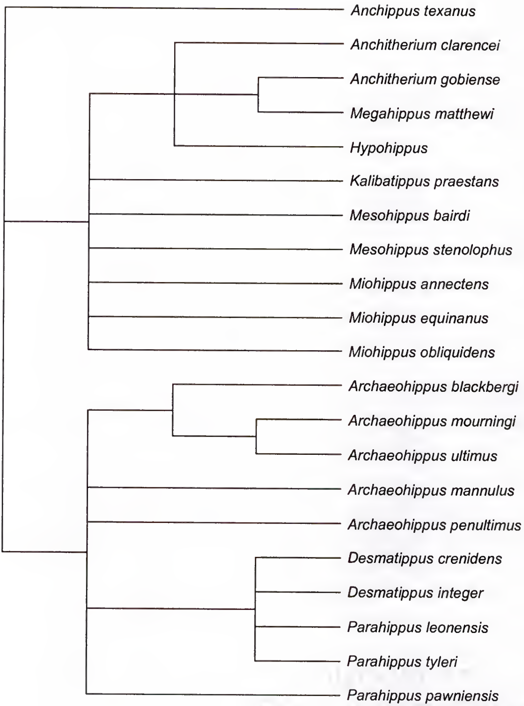


FIGURE 25. Strict consensus tree of anchithere relationships without the constraint of an outgroup.

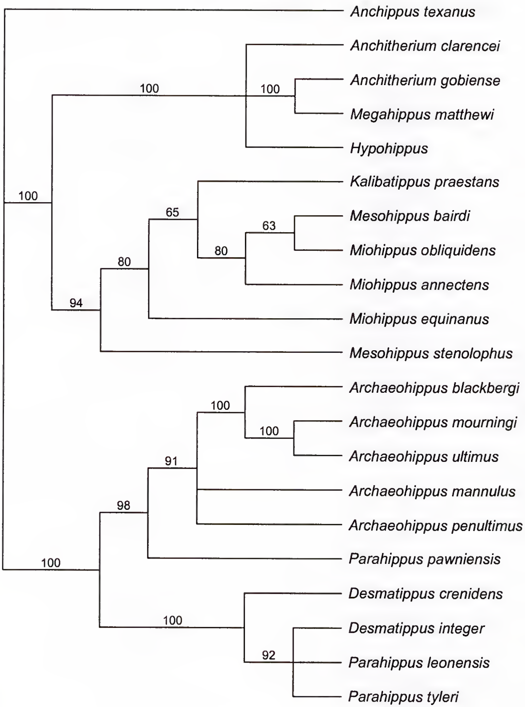


FIGURE 26. Majority-rule consensus tree of anchithere relationships without assignment of an outgroup. Numbers indicate percent of retrieval of topology at each node.

the most basal position the clade, and *A. clarencei* moves out of the ASS. Intriguingly, *A. gobiense* remains deep within the ASS clade, paired with *M. matthewi*.

In no tree was *M. stenolophus* placed within or near the *Archaeohippus* clade. A tree four steps longer than the shortest trees is formed by the placement of *M. stenolophus* at the base of the *Archaeohippus* clade. This contradicts the assignment of *M. stenolophus* to *Archaeohippus* by Storer and Bryant (1996). It is, perhaps, justifiable to assign it to *Miohippus*. Postcranial data such as the phalangeal indices, which are not available, would best resolve this taxon's relationships.

The relationships of the ingroup are as fascinating as those of the outgroup. *A. ultimus* and *A. mourningi* are upon visual inspection, almost indistinguishable. This fact is supported by every cladistic analysis in the present study. *A. ultimus* has been found in Oregon (Downs, 1956) and Montana (Douglas, 1903) from the early Barstovian, while *A. mourningi* from California (Bode 1933) is late Barstovian. These two species may be regional/temporal variants of a single form. At present, the utility to biostratigraphic studies of maintaining these as separate species may outweigh the benefits to taxonomy of synonymizing them. Pending further study, these taxa will be considered distinct.

In most cases, the sister taxon of the clade formed by *A. ultimus+A. mourningi* is *A. blackbergi* from the early Hemingfordian of Florida (White 1942) and Texas (Forsten, 1975). This clade is retrieved by the bootstrap analysis (Fig. 22) and by all consensus trees (Figs. 23, 24, 25, 26). *A. penultimus* from the late Hemingfordian of Nebraska (Matthew, 1924), is external to this clade and, in most of the heuristic analyses, pairs with *A. mannulus* from the Arikareean of Florida (O'Sullivan, 2002). This relationship is not retrieved by the strict consensus or bootstrap analyses. The *Archaeohippus* clade is

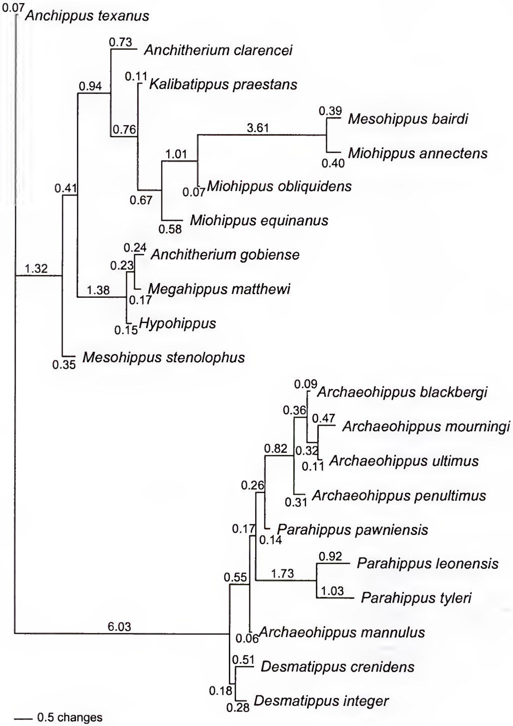

0.07 Anchippus texanus
0.73 Anchitherium clarencei
0.11 Kalibatippus praestans
0.94
0.76
3.61
0.39 Mesohippus bairdi
0.40 Miohippus annectens
1.01
0.07 Miohippus obliquidens
0.41
0.67
0.58 Miohippus equinanus
0.24 Anchitherium gobiense
0.23
1.32
1.38
0.17 Megahippus matthewi
0.15 Hypohippus
0.35 Mesohippus stenolophus
0.09 Archaeohippus blackbergi
0.36
0.47 Archaeohippus mourningi
0.82
0.32
0.11 Archaeohippus ultimus
0.26
0.31 Archaeohippus penultimus
0.17
0.14 Parahippus pawniensis
0.92 Parahippus leonensis
0.55
1.73
1.03 Parahippus tyleri
6.03
0.06 Archaeohippus mannulus
0.51 Desmatippus crenidens
0.18
0.28 Desmatippus integer
0.5 changes

FIGURE 27. Heuristic analysis with each character weighted according to its Consistency Index. Numbers represent rescaled branch lengths.

supported in 95 of 106 heuristic analyses. In 11 trees, this clade is made paraphyletic by the removal of *A. mannulus* to a position as sister taxon to the *Desmatippus/Parahippus* clade (Fig. 20). The mobility of *A. mannulus* in these trees is similar to that of *K. praestans*, which is considered the most primitive member of the ASS clade (MacFadden, 2001). This could be a characteristic of the matrix, where the most primitive members of strongly defined crown clades tend to drop back into the more broadly defined clades from which the crown clade arose. Thus, *A. mannulus* demonstrates that it is almost as clearly a dwarf species of *Desmatippus* as it is the earliest known species of *Archaeohippus*.

The placement of *P. pawniensis* is intriguing. In bootstrap and consensus trees (Figs. 22, 23, 25), it falls into the poltomy that surrounds the *Archaeohippus* and *Desmatippus/Parahippus* clades. In trees from the initial and weighted heuristic analyses (Figs. 19, 20, 21, 27), *P. pawniensis* is the faithful sister of the *Archaeohippus* clade, even when *A. mannulus* is not (Fig. 20). This latter fact is probably due to missing data. *P. pawniensis* has a deep lacrimal fossa (as in *Archaeohippus*, although it lacks the deep malar fossa), and the available material for *A. mannulus* lacks the facial region entirely, so no data were coded for its facial fossae. Nevertheless, it raises the interesting question of whether to include *P. pawniensis* in the genus *Archaeohippus*, since it clearly has less affinity for the *Desmatippus/Parahippus* clade. It requires three additional steps to place *P. pawniensis* within the *Desmatippus/Parahippus* clade, and a tree eight steps longer than the shortest trees is required to place *P. pawniensis* as the sister taxon of *P. leonensis+P.tyleri*. Such a move might involve not only *P. pawniensis*, but the possibly closely related *P. atavus* and *P. pristinus*.

Conclusions

This study will be greatly enhanced with the addition of more species presently assigned to *Mesohippus* and *Miohippus*. It seems unlikely that these taxa will be sorted along the criteria of Prothero and Shubin (1989), with all miohippines readily distinguished by possession of long faces and cuboid facets. The type species *Mesohippus bairdi* and *Miohippus annectens* form a clade with *Miohippus obliquidens* in 54% of the bootstrap replicates (Fig. 22) and 80% of trees without outgroup in the majority-rule consensus analysis (Fig. 26). These clades do not include other species of *Mesohippus* or *Miohippus*. Again, these could be artifacts of the matrix. Alternatively, these patterns could indicate that there is at least one unnamed genus in the analysis less closely related to these species of *Mesohippus* and *Miohippus* than these taxa are related to each other. The possibility exists that *M. bairdi* is too derived a species to adequately represent the mesohippines. If this were the case, *M. bairdi* would become a species of *Miohippus* since *Miohippus* (Marsh, 1874) has precedence over *Mesohippus* (Marsh, 1875), and a new type would be assigned. This redesignation will not be necessary as inclusion of more primitive mesohippines will further resolve relationships.

The study has clear implications for the origin of *Archaeohippus*. At this point in the study, not one of these taxa is a strong candidate for ancestor of the *Archaeohippus* clade. The most primitive *Archaeohippus*, *A. mannulus*, may be a dwarf desmatippine. If future studies do not assign *P. pawniensis* to *Archaeohippus*, the likely alternative is that it will be assigned to *Desmatippus*. The last ancestor it shared with *A. mannulus* may be close phylogenetically (and chronologically) to the White Springs equid, which was present in the Gulf Coast region during the Arikareean.

This study brings greater resolution to the phylogeny of the ASL equids. This group is a major component of Holarctic terrestrial biomes throughout the middle Cenozoic. This period saw the decline of the Eocene forests in North America, the spread of open forest/savanna ecosystems in the Oligocene, and the advent and expansion of grassland ecosystems in the Miocene. The evolutionary history of equids reflects the coevolution of this group throughout this period of global climate change. The better we understand this coevolutionary sequence the better will be our ability to predict the adaptive responses of ungulates to ecosystem change.

CHAPTER 6
SUPPOSITIONS AND CONCLUSIONS

The anchithere radiation has been viewed as the origination and diversification of taxa from the Oligocene genus *Miohippus*. This diversification resulted in at least three lineages that culminated in distinct ecomorphs: a large, low-crowned, fully tridactyl form ("Anchitheriinae" *sensu stricto*); a medium-sized, more high-crowned form with reduced tridactyly (*Parahippus*); and a small, brachydont form with reduced tridactyly and a very deep malar fossa (*Archaeohippus*). *Anchitherium* is much larger than advanced species of *Miohippus*, early species of *Parahippus* are only slightly larger than advanced *Miohippus*, and *Archaeohippus* is much smaller (with the possible exception of *M. equinanus*) than any species of *Miohippus*, about the size of *Mesohippus*. The members of the anchithere radiation all share a metaloph connected to the ectoloph. Discerning the exact pattern of this radiation is difficult. The intermediate morphologies of taxa from the Arikareean suggest complex interrelationships of genera that are quite distinct by the Hemingfordian. Some of these intermediate forms have been assigned to *Parahippus*, *Desmatippus*, *Anchippus*, or merely "equid of anchithere grade" in museum collections. In addition, some species of *Miohippus* possess connected metalophs on deciduous premolars only, others on permanent premolars only, and still others on molars only. This suggests that the character state "metaloph connected to the ectoloph" may have evolved in parallel from several *Miohippus* ancestors. However, pending further study, it seems likely that the last common ancestor of the three main lineages of the anchithere radiation possessed a connection between the metaloph and ectoloph on all or most of its cheekteeth. Therefore, the last common ancestor of *Archaeohippus*, *Parahippus*, and *Anchitherium* was, by definition, not a species of *Miohippus*. It was an anchithere horse of medium size with brachydont teeth. Unless the functionally tridactyl limbs of the ASS are the result of an evolutionary reversal, this common ancestor also possessed functionally tridactyl limbs.

Although *Archaeohippus* is generally considered to be a dwarf genus, the younger species tend to be larger than *A. mannulus* and *A. blackbergi*. This contrasts with the trend seen in the fossil record of the Barstovian-Hemphillian dwarf equid genus *Calippus*, which displays size reduction in a sequence of species (Hulbert, 1988, 1993). *A. blackbergi* from the early Hemingfordian was smaller than *A. penultimus* from the late Hemingfordian of Nebraska. *A. ultimus* and *A. mourningi* from the Barstovian of the American west were larger than *A. penultimus*. Thus, after an initial reduction in body size in this genus during the Arikareean, further evolution of *Archaeohippus* follows Cope's Rule. The exception to this pattern is *A. stenolophus*, a recently described Hemingfordian species that is larger than any other species of *Archaeohippus* (Storer and Bryant, 1993). However, the implications of its large size and the *Miohippus*-like aspect of its tooth morphology (Storer and Bryant, 1993, Fig. 3) require further investigation of this species before it can be clearly assigned to *Archaeohippus*.

Dwarfing and the Gulf Coastal Plain

The endemic taxa of the Gulf Coastal Fauna of the Arikareean includes several dwarves: *A. blackbergi*, the amphicyonid *Daphaenodon notionastes*, a dwarf rhinoceros, and a dwarf camel (Albright, 1998). To this list can be added the tiny species of

Archaeohippus represented by UF 160784. Explanations of body size reduction in mammalian taxa usually evoke one of the following biogeographic principles. As discussed by Frailey (1980), small body size in Gulf Coast Fauna mammals during the Arikareean could be a manifestation of Bergmann's Rule. This rule states that average body mass for members of a species is greater in higher latitudes, where the lower surface-area-to-volume ratio would encourage retention of metabolic heat. Thus, horses living nearer the equator should be smaller than those living in the Great Plains. Some researchers have questioned whether this trend is pervasive enough to consider it a predictive rule (McNab, 1971; Geist, 1987).

An alternative to Bergmann's rule, also suggested by Frailey (1980), is dwarfing due to the selective regime of insularity. The rather sudden appearance of a diverse group of mammalian dwarves, including this tiny species of *Archaeohippus*, suggests an environment imposing very strong directional selection for reduction of body size. Islands are known to produce endemic giants and dwarves (Sondaar, 1977), although the reason for this is a topic of debate (Roth, 1990). In his article on the subject, Sondaar (1977) noted several common trends among island herbivore dwarves:

1. Insular dwarves tend to display increased hypsodonty, possibly as an adaptation to an abrasive diet. In the case of Sondaar's Mediterranean island endemics, hypsodonty may be an adaptation to the volcanic soils of these islands. While hardly a hypsodont animal, the tendency for *Archaeohippus* to have relatively tall teeth for its body size has been noted (Bode, 1933). This agrees with Gould's (1975) assertion that dwarfing affects the teeth to a lesser degree than other skeletal elements, resulting in relatively large teeth.

2. Limb proportions tend to shift to low gear, that is, distal elements become relatively short. The opposite is true of *Archaeohippus*. However, the islands to which Sondaar's (1977) dwarves had adapted were mountainous, and low gear locomotion in small ungulates is usually an adaptation to uneven terrain. Such a terrain is not plausible for Arikareean Florida.

3. Size variation within island populations is greater than in mainland groups, probably as the result of a shift in selective pressures. If UF 182408, a lateral first phalanx (16.85 mm long) of *A. mannulus* that was recovered from the dredge site represents the upper end of the size range, then a comparison with the lateral phalanx of UF 160784 (10.9 mm, only 65% the size of the larger specimen) suggests a large range of variation was present in this population. Body size variation in mammal populations is often due to sexual dimorphism. However, though *A. blackbergi* from Thomas Farm demonstrates dimorphism in canine size (a sexually dimorphic trait in horses), and body size range is large, canine size and body size do not correlate (O'Sullivan, 1998). Thus, there is no evidence of sexual dimorphism in body size in early species of *Archaeohippus*.

The idea that the character and composition of the Gulf Coastal Fauna was influenced by an island Florida was first raised by White (1942), who studied geological maps to determine the known extent of limestone sediments in Florida. White's reconstruction is as follows: At the close of the Eocene, crustal movements caused the Central Florida Dome to rise above sea level. These same tectonic forces caused northern Florida to drop, forming the Okefenokee Trench (the Georgia Channel of Randazzo, 1997). Subsequent crustal activity and eustatic sea level changes resulted in periods of isolation of central Florida as the Okefenokee Trench was filled by the sea, forming a strait 80 to 160 km across. During the early Oligocene, when the Marianna Limestone was being deposited, the Okefenokee Trough formed a waisted isthmus with bays to the east and west. Towards the end of the early Oligocene, the bays on either end of the strait connected to form a channel upwards of 80 km wide. At this time, the Glendon limestone was deposited across north Florida. Toward the end of this period of limestone deposition, island Florida reattached to the mainland. With the deposition of the Suwannee limestone in the late Oligocene came another period of isolation for a greatly reduced Florida. At this time, the channel would have been nearly 240 km wide. Formation of the Chattahoochie Anticline in southern Georgia constricted the channel, which filled with sediment and became a landbridge from the end of the Oligocene.

Subsequent geological work (for a review, see Randazzo and Jones, 1997) has cast doubt on the role of frequent episodes of tectonic activity in the formation of Florida during the Cenozoic. Also, stratigraphic resolution has improved, and many more limestone formations have been identified. However, the general pattern depicted by White (1942) is corroborated. The Florida sedimentary platform was isolated from the mainland throughout most of the Paleogene by a deep-water channel. By the end of the Oligocene, this channel was filled by clastic sediments from the continent following a sea-level low stand (Scott, 1997). Terrestrial mammal faunas appearing in Florida at this time may have experienced insularity due to periodic increases in sea level.

Geological studies indicate that Florida formed as a limestone platform separated from the mainland by the Suwannee Straits, a deep water channel perhaps in excess of 60 km wide (Randazzo, 1997). During the first half of the Oligocene, sea level rose to well

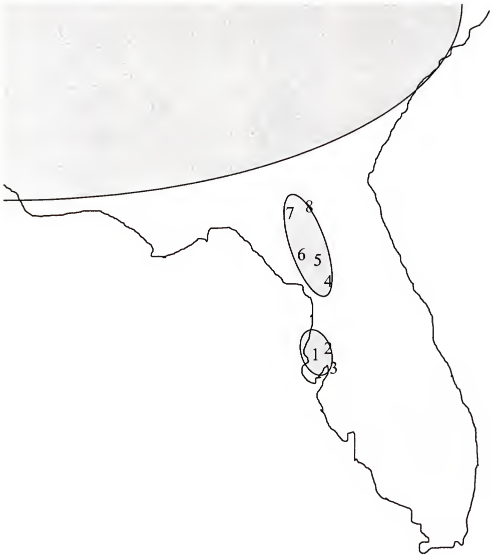


FIGURE 19. Speculative reconstruction of Florida in the early to late-early Arikareean, with present-day outline superimposed. Sea level increase in the late Oligocene reduced Florida from a small peninsula to one or more small islands. Sites included on this map are (5) the Whitneyan I-75 site, and the Arikareean sites (1) Curlew Creek, (2) Brooksville, (3) Cowhouse Slough, (4) Martin-Anthony, (6) Buda, (7) Live Oak, (8) White Springs.

above present sea level. However, in the latter half of the Oligocene, sea level dropped well below present sea level, then attained levels close to that of the present, then dropped and rose again. During the first sea level low stand, the limestone platform appeared above sea level and the channel began to fill with clastic sediments from the continent (Scott, 1997). Sometime in this period, the island would have become accessible to large mammals; perhaps it was a peninsula. Prior to the complete infilling of the channel, periodic sea level high stands would have isolated the Florida platform, possibly more than once (Fig. 19). Terrestrial mammal faunas in Florida during such periods of isolation would then be exposed to and adapt to the insular selective regime. Simultaneous size reduction of various taxa would occur. The subsequent sea level low stand during the late Arikareean reformed the Florida peninsula, and dwarf taxa could colonize the mainland.

Conclusions

The results of this study suggest the following:

1. Specimen UF 160784 is the holotype of the most primitive known species of *Archaeohippus*. The dentition and pedal adaptations of this species link it with both *A. blackbergi* and *P. leonensis*.

2. The life table analysis of the population of *A. blackbergi* from Thomas Farm (Fig. 3) indicates that this taxon differed from the sympatric equid *Parahippus leonensis* in maturation rate, potential longevity, and tooth wear rate. The latter suggests differences in dietary behavior. Also of note is the lack of sexual dimorphism in *A. blackbergi* and the presence of a sharp increase in age-dependent mortality in young adults that may be attributable to male combat.

3. An analysis of stable isotopes from equid tooth enamel failed to corroborate hypothesized dietary differentiation between *A. blackbergi* and *P. leonensis* that was suggested by the tooth wear data. Although *A. blackbergi* does demonstrate faster development than does *P. leonensis*, its ontogeny was actually longer than that of the Oligocene equid *Miohippus obliquidens*. This does not support hypothesized progenesis in the *M. obliquidens--A. blackbergi* morphocline. However, results from the phylogenetic analysis suggest that *Archaeohippus* is the sister taxon of some species of primitive parahippine in the genus *Desmatippus*. Members of this genus are almost all larger than *Archaeohippus*, and probably similar to *P. leonensis* in duration of ontogeny. Therefore, the future use of an as-yet-unidentified better candidate to represent the ancestral morphotype of *Archaeohippus* may yield results that support the hypothesis of reduction of ontogenetic timing in the evolution of reduced body size in this genus.

4. A cladistic analysis of the species of *Archaeohippus* and related taxa defends the monophyly of the genus. It nests the *Archaeohippus* clade within the clade of equids that also includes species assigned to *Desmatippus* and *Parahippus*, all of which have elongated phalanges.

5. The record of a dwarf horse in peninsular Florida during the Arikareean plus the presence of several conspicuous dwarf taxa in the Gulf Coast Fauna of the early Miocene may result from a period of insularity. Early in the terrestrial phase of Florida, mammals colonized the Florida platform. Subsequent to this colonization, Florida became isolated from the mainland by a wide marine channel. Insularity caused dwarfing in at least one population of horses. The result was the tiny species *Archaeohippus mannulus*, possibly

the first appearance of this genus. By the early Hemingfordian, *Archaeohippus*, in the form of *A. blackbergi*, was introduced to the mainland.

Future directions for this study include:

1. More taxa and characters will be added to the phylogenetic analysis. The question of paedomorphosis can not be addressed fully in the absence of an identified ancestor for *Archaeohippus*. For example, paedomorphosis involves a change in morphology in the descendent species relative to the ancestor. Although *Archaeohippus* appears to be juvenilized in its skeletal proportions, that can not be demonstrated without knowing the ancestral morphology. Also, further resolution of the relationships of the species presently assigned to *Mesohippus* and *Miohippus* would prove useful to our overall understanding of horse evolution and paleobiogeography.

2. The fauna associated with *Archaeohippus mannulus* will be described in order to better characterize what is one of the earliest terrestrial vertebrate assemblages in Florida. This effort may lend credence to the suggestion that *Archaeohippus* evolved in Florida during a period of island endemism.

3. More life table analyses of populations of primitive parahippines will be performed to determine whether the mortality spike among young adults is common among these animals, thus tracing the evolution of this social behavior in the Equidae.

4. Further isotope microsample studies on animals with known life histories will be performed in order to detect the influence of such variable as weaning stress, which may introduce a false seasonal signal in carbon ratios. In addition, I intend to perform tooth microwear studies in order to better ascertain diet in extinct ungulates.

This study is significant in that it employs a variety traditional and new techniques to add to our knowledge of the evolutionary history of the Equidae, one of the classic textbook examples of vertebrate evolution. In particular, the analysis of serial microsamples of tooth enamel obtained from complete cheek tooth rows is unique in the number of samples taken from each specimen, the number of specimens and taxa included, and the variety of questions addressed with the data.

This study better characterizes the earliest period of one of the most successful adaptive radiations of large terrestrial mammals. This is a particularly important period of horse evolution, during which horses were diversifying in response to ecosystem evolution. Thus, it gives us a better sense of how ungulates respond to global change, and may aid scholars interested in predicting future responses by ungulates to present trends of global change.

APPENDIX
COMPARISONS OF KEY TAXA

Prothero and Shubin (1989) claim that there is no morphological overlap between *Mesohippus* and *Miohippus* species and that *Miohippus* skulls have longer faces and longer/deeper facial fossae. Measurements taken from the photos they provide falsify this statement. There is enough overlap to cause one to doubt their very strong assertions, which are constructed as support for the model of punctuated equilibria (Eldredge and Gould, 1972).

Skull elongation in Oligocene equids as an evolutionary trend is an extension of ontogeny, a form of peramorphosis. It resulted in the anterior orbit shifting from a position over the M1 in *Mesohippus* to over the M2 in *Miohippus*. Also affected is the morphology of the zygomatic arch. In occlusal view, the zygomatic of *Mesohippus* extends rostrally as far as the M1/P4. In *Miohippus*, the zygomatic tapers to the M2/M1 junction. In *Mesohippus*, the rostral extent of the zygomatic is inflated and tapers gradually; in *Miohippus*, it is narrow and ends abruptly. The posterior border of the anterior masseteric shelf of the zygomatic (herein referred to as the zygomatic notch) lies next to the M3 in *Mesohippus*, but behind the M3 in *Miohippus*. The preorbital fossa is present in *Mesohippus* but not as concave as in *Miohippus*. *Miohippus* species usually have a pinched, rimmed area directly in front of the orbit. UF 200375 from the Orellan Turtle-Oreodont Zone, Brule Formation, Sioux County, Nebraska, was assigned to *Miohippus* sp. based on its possession of the *Miohippus* condition in these cranial and pedal characters. *Mesohippus eulophus* was placed in *Miohippus obliquidens* by Prothero and Shubin (1989). Based on its orbit and zygomatic positions, I'd say that it is in fact *Miohippus*.

Regarding the facial fossa, as is generally understood, the malar facial fossa includes the maxilla, jugal, and lacrimal just dorsal to the facial (or malar) crest. The lacrimal or dorsal preorbital fossa includes the maxilla, nasal, and sometimes lacrimal bones. *A. mourningi* and *A. ultimus* both possess preorbital fossae that are more deeply pocketed than *A. blackbergi* and perhaps more so than *A. penultimus*. In Thomas Farm *A. blackbergi*, the lacrimal and malar fossae are equally deep, not too deeply pocketed, and do not come down right over molar roots. The preorbital bar is thin. Some individuals have tapering jugals (*Mesohippus*-like), while some have truncated jugals (*Miohippus*-like). The zygomatic notch is behind the M3. The infraorbital foramen is above the posterior P3. Orbit is over posterior M2 or anterior M3.

A. penultimus has a distinct ridge between lacrimal and malar fossae. Malar is deeply pocketed and closely approaches second molar roots. Preorbital bar is thicker than in *A. blackbergi*, probably because the malar fossa is deeper and lower. Tapering jugal, and zygomatic notch behind M3. Infraorbital foramen over anterior P3 with the orbit over M2.

A. ultimus has a very deeply pocketed malar that comes right down on the roots of the third molars. The preorbital bar is similar to *A. penultimus*. The sides of the fossa are very straight. The jugal is truncated and the zygomatic notch is far behind the M3. The infraorbital foramen is above the anterior P4, and the orbit is over M3.

A. mourningi has very deep pocketing, though with perhaps more equality between lacrimal and malar fossae. The malar fossa does not penetrate as low over the molars as in *A. ultimus*. This species has the thickest preorbital bar of all *Archaeohippus*. Foramen over anterior P4 and orbit over M3.

AMNH 111743 (cast of LACM 400/5304) is *A. mourningi* from Punchbowl, CA. AMNH 8174 is *A. ultimus* from Mascall, OR. Without larger samples with which to assess intraspecific variation, it is not possible to determine whether or not these two specimens may belong to the same species. Thus, the validity of *A. mourningi* will not be challenged at this time.

Perforation of protoloph may correlate with metastyle development. *A. blackbergi* tends to has less occurrence of perforated protoloph, and it has very strong posterior styles. *Archaeohippus* has large, distinct styles as seen in *A. blackbergi*, *A. penultimus*, and *A. mannulus*. The metastyle is less intrusive in this state. In some cases it clearly perforates the protoloph, but less so than in most *Miohippus* species.

Miohippus equinanus AMNH 39028 has metastyle perforating the protoloph of succeeding tooth. The enamel rolls over into the perforation. Also, the postfossette is not closed by the hypostyle as in *Archaeohippus*. This is an important distinguishing character.

In *Hyracotherium* sp., AMNH 2898, mesostyles and metastyles are not present. Specimen includes upper and lower jaws from the Eocene Wasatch Formation of the Big Horn Basin, Wyoming. Ectoloph ribs represent the original paracone and metacone, so they are very primitive within the Equidae. The styles, on the other hand, are derived sequentially over the first thirty million years of equid evolution. In AMNH 2898, the parastyle and paracone are strong. Incipient mesostyle on M2. Metacone weak, especially on M3. Lower dentition has m3 with a huge hypoconulid heel with large central basin. Therefore, the heel and the centralized basin are primitive for equids.

Orohippus agilis AMNH 12649 upper and lower teeth from the Eocene Bridger Formation Bed C5 Sage Creek, Bridger Basin, WY. Mesostyle better developed on M2 and M3 than in *Hyracotherium*. Metacone is stronger than in *Hyracotherium*.

Epihippus gracilis AMNH 2036 includes a mandibular toothrow, an upper M3 and I1 from the Uinta Formation, Base C Beds, White River, Utah. It displays well-developed mesostyles. In *Hyracotherium*, *Orohippus*, and *Epihippus*, the metastyle is not present. The tooth row of *Hyracotherium* is straighter than those of the later forms. The condition whereby the metacone tips into and perforates the protoloph, forming Skinner's "parastyle cleft", starts with *Orohippus* and *Epihippus* which possess squarer teeth in a close-packed, curvilinear row.

Mesohippus has all three styles clearly present. Strengthening of the parastyle of dP2 creates a more advanced, triangular shape than seen in P2. Orbit is over M1 or M2 in adults. MTIII/cuboid contact facet appears to be lacking in most specimens, although a clear facet is present in some specimens of the type species *M. bairdi*.

The anterostyle of P2 is undeveloped in *Mesohippus* and most *Miohippus*, nor is it present in *M. equinanus* or *P. pristinus*. It is present in all species of *Archaeohippus*, although strongest in *A. mannulus*, *A. blackbergi*, and *A.ultimus*.

On the paratype of *Archaeohippus penultimus* (AMNH 18951) from Sheep Creek, NE one can observe a slight trace of the gutter between the cristid obliqua and the metaconid-metastylid, thus, the cristid obliqua is not connected to the metastylid in early wear. The separation is slightly more so than in *Archaeohippus blackbergi*. A. *penultimus* F:AM 71650 has no connection of metaloph to the ectoloph on M2 and M3.

A. blackbergi has hypocone frequently surrounded by a medivalliconule not seen in *A. penultimus*, which has fuller hypocone (although one P3 has a tiny medivalliconule arising from the distinct lingual cingulum). The lingual projection of the hypostyle (which I call Hypostyle Process C and White [1942] identified as the hypostyle itself) is present in *A. penultimus* and connects with the cingulum around the base of the hypocone.

The distinctions observed by Bode (1933) are generally true of a comparison of any *Archaeohippus* dp2 vs. p2. The metaflexid of the deciduous tooth has a more oblique internal angle. This tends to elongate the tooth. Such elongation is variably present in the adult p2 of *Archaeohippus*, and is similar to a trend seen in the adult dentitions of equids of merychippine grade, thus suggesting a phylogenetic link between *Archaeohippus* and more derived equids.

The p2 in *Archaeohippus* is longer than in earlier horses, especially *Mesohippus*. The trigonid is much more fully developed and the orientation of the protoconid is more anterior. Elongation of the P2/p2 is a more informative example of character evolution than is reduction of the M3, which seems to exhibit greater homoplasy and less functional significance. The p2 is the only lower cheektooth to possess a paraconid, as opposed to merely a paralophid. When the lingual cingulum rises strongly up the anterior edge of the paraconid, it forms a pointed cristid. This cristid is larger in *Archaeohippus* than in either *Mesohippus bairdi* or *Miohippus obliquidens*.

The paraconid in *Mesohippus bairdi* is much smaller than the protoconid, which dominates the trigonid. The labial surface of the protoconid is rounded and forms a bladelike edge similar to that of an incisor. The protocristid connects the protoconid to the metaconid at about the same angle that a cingular cristid ascends from a position posterior and lingual to the protoconid. The result is an occlusal pattern of a three rayed equilateral star, with the crown of the protoconid central. The metaflexid is shallow. The cristid obliqua connects anterolabial to the metaconid, and low.

The relative size of the paraconid is slightly greater in *Miohippus obliquidens*. The labial surface of the protoconid is slightly concave anterior to its apex. The position of the protocristid is similar, but the cingular cristid is directed less posteriorly than in *M. bairdi*. The metaflexid is more concave. The cristid obliqua still connects anterolabial to the metaconid, and is taller, but the uppermost part of the cristid obliqua is retracted from (not in connection with) the metaconid.

In *Archaeohippus*, a strong concavity on the labial surface of the protoconid between the columns of the protoconid and paraconid reduces the size of the protoconid and donates some of its original volume to the paraconid, which is nearly as large as the protoconid. In *A. mannulus*, the labial side of the paraconid is flat, not as swollen as in *A. blackbergi*. The cingular cristid is still distinct and sharp in *A. mannulus*, but only on the lower half of the tooth does it decline posteriorly; the upper half is directly labial. In *A. blackbergi*, this area is less distinct, the column of the protoconid is rounded with a gentle porterior decline toward the base. The metaflexid is deeply concave. In both of these species, the cristid obliqua connects directly to the metaconid and high.

The present author has observed that in all species of *Archaeohippus* metaconid-metastylid twinning is weak, confined to the top millimeter or two of p3-m3. Twinning is strongest on the dp2, whereas the p2 usually lacks the metastylid entirely.

A. blackbergi FGS V-6374 has M1-M3 = 33.2 mm; M3/M1-M3 index = 0.30; *Miohippus* sp. UF 200375 has M1-M3 = 37 mm and index= 0.41; *Mesohippus bairdi* from Goshen MCZ 20475 has M1-M3 = 33.9 mm and an index = 0.36 and *Mesohippus* sp. UF 111799 from the Brule Fm. of Badlands National Park, SD has M1-M3 = 34.6 mm, index = 0.35. This confirms the pattern detected by Forsten (1973) that *A. blackbergi* has a reduced M3 relative to the condition in *Mesohippus* and *Miohippus*. Species of *Miohippus* tend to have elongated M3/m3 relative to *Mesohippus*.

According to Osborn (1918) the hypostyle shape in *Mesohippus* is variable; in *Miohippus* it is large, angular, and separate from post-cingulum; in *Parahippus* it is prominent, subtriangular, and can close the postfossette.

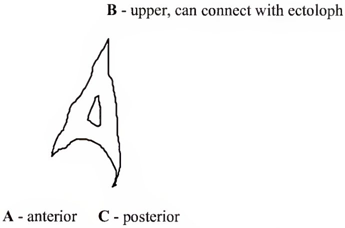


FIGURE 28. Diagram of the parts of the triangular "Type 3" hypostyle found in *Archaeohippus* and *Parahippus*.

In *A. mannulus*, the large, triangular hypostyle (Fig. 1) closes the postfossette with with a connection of Part A to the metaloph in all teeth in the type specimen, a connection of Part B to the ectoloph in most teeth, and Part C is very strong. *A. blackbergi* is similar to *A. mannulus*. *P. leonensis* has a strong connection A to the metaloph and of B to the ectoloph, but C is reduced by the posterior expansion of the hypocone. In *Anchitherium clarencei*, A, B, and C are strong.

Lower cheek teeth of *A. blackbergi* are less enclosed lingually by their lophs than are cheek teeth of more primitive forms. The paralophid curls in and is taller and thicker in primitive forms, filling the trigonid.

Observations on the Postcranial Skeleton

The scapular glenoid fossa is rounded in *A. blackbergi* from Thomas Farm and much more elongate in *Miohippus obliquidens* from the Harvard Fossil Reserve. There also is an individual with what is probably a pathology - a highly constrained glenoid fossa (very thick rim) and a broken, possibly healed acromion process.

The proximal third phalanx of *Archaeohippus blackbergi* has a strong proximal prominence (cruciate scar) as in some *Mesohippus*, *Anchitherium*, and *Merychippus* (as seen in Camp and Smith, 1942). The lateral volar scar is also quite strong in *A. blackbergi*.

The calcaneum has a pit behind the processus cochlearis in *Archaeohippus blackbergi*, *Orohippus*, *Epihippus* and to a lesser degree in *Parahippus leonensis* from Thomas Farm. This may be a locking position for hyperextension of the ankle (bipedal stance as in the duiker). In *A. blackbergi* from Thomas Farm the oblong facet is well separated form the mesiodistal facet, usually more so than in *P. leonensis*. The cuboid facet has a distinct non-articular (ligament attachment scar) zone not seen in *P. leonenesis*, which has a continuous medial border of the facet even though part of the facet may not articulate.

The astragulus neck in *A. blackbergi* is slightly relatively longer than in *Parahippus*. Cuboid facet is relatively larger. Posteromesial calcaneal facet of the astragulus is convex distally and wraps up toward the distal navicular facet. In *P. leonensis* the facet is flatter and more separate from navicular facet.

P. leonensis: cuboid facet tends to be more cranially placed than in *A. blackbergi*, though about 3/10 are as in *A. blackbergi*.

On the MC III of *P. leonensis* the volar tubercle is usually subtle, or, if distinct, it is small; large upper facet for unciform with smaller facet below it for MC IV; posterior facets above and below each other are roughly equal in size. *A. blackbergi* usually has a large volar tubercle; facet relative sizes are similar to *P. leonensis*. Distal MC III the articular condyles flare down and out more in *P. leonensis* than in *A. blackbergi*.

Anchitherium clarencei from Thomas Farm has a large mesentocuneiform facet that angles upward; anterior and posterior facets for MT II small; MT IV facets are small considering body size, so lateral metapodials had good purchase on the tarsals above. MT III is not well attached and providing support to, or being supported by, the laterals. This may explain why MT III has a mesentocuneiform facet, a fact that perplexed Hussain (1974) since this character is seen mostly in horses tending toward monodactyly. Each metapodial must independently support the animal's weight, with most weight going to MT III. Such an arrangement provided strong support without sacrificing flexibility.

Observations on Some Very Early Florida Equids

The I-75 site (Patton, 1969) of Alachua County, Florida has one upper molar (UF 208904) and an uncatalogued lower molar that are almost certainly specimens of *A. blackbergi* that were accidentally misplaced from the Thomas Farm collection (Gary Morgan, pers. comm. 2001). However, an unworn upper molar (UF 171282) lacks a metaloph connection, though the crista from the metaloph approaches the crista from the ectoloph. It lacks the advanced state of the hypostyle-it doesn't close off the postfossette, and there is no tiny fossette in the triangle of the hypostyle. Such a simple hypostyle is also present in *A. mannulus* and *A. blackbergi* in the M3. One worn lower molar has a higher crown height than *Archaeohippus*. The base of the metaconid is plump as in *Miohippus*.

The fossil equids of the Brooksville II (Hayes, 2000) site have 1) lower molars less like *A. blackbergi* than the small (probable Thomas Farm) specimen from I-75, 2) broad, blade-like entoconid, 3) projecting hypoconulid, 4) metaconid/metastylid narrow and twinning very strong, 5) cristid obliqua deeply retracted from metastylid, 6) protolophid wraps back to connect metaconid posteriorly; this along with twinning, suggests *Miohippus*. *A. blackbergi* has a broad protolophid/metaconid connection and a broad metaconid/metastylid base that prevents the protolophid approaching the metaconid from behind. Lophids even sharper and more v-shaped than in *A. blackbergi*. Strong vertical lines in enamel. Very little difference in lingual vs. labial profile; in *Archaeohippus* the lingual profile is much lower than the labial. Patella has a hook as in *A. mannulus*. Astragulus notch is shallower; neck longer than in *A. blackbergi*. Proximal phalanx III has less distinct keel groove in proximal articular surface. Distal surface less grooved and separate than *Archaeohippus*.

Brooksville II lower cheek teeth are distinct from *A. mannulus* and *A. blackbergi*. They are 1) larger; 2) labial sides of lophids are more pinched; 3) lingual sides of lophids are wider.

UF 156377 is a Rp2 that is very distinctive, large, primitive. It may be deciduous; it is different, nonetheless. UF 156370 looks like a deciduous PM. If so, it is more advanced than the very primitive deciduous PMs from the I-75 site in that it has 1) nearly complete hypostyle; 2) nearly connected metalophid; 3) very distinct protocone, incomplete protoloph; 4) weak metastyle. UF 156372 RM1 has 1) very low crown height (like a deciduous tooth); 2) very weak metastyle; 3) connected metaloph; 4) small medivalliconule. UF 156378 adult RM1 1) weak metastyle; 2)very low and thin metaloph connection; 3) strongly perforated protoloph; 4) triangular hypostyle starting to close off postfossette; 5) protoloph not as strong as I-75 *Archaeohippus* (or *A. blackbergi* or *A. mannulus*); 6) metaconule small and indistinct so the metaloph is a smooth curve. In these details, the Brooksville equid is more primitive than *Archaeohippus*.

The Cowhouse Slough (Morgan, 1989) equid was identified by Webb et al. (1995) as *Archaeohippus* because its teeth are small and low-crowned possesses a connection of metaloph and ectoloph. This assignment thus places the earliest *Archaeohippus* material in Florida in the Arikareean. As with the equids from Brooksville, the Cowhouse Slough equids superficially resemble *Archaeohippus*, but they lack the derived character states present in all members of that genus. The teeth from Cowhouse Slough have primitively low, broad, conical protocones and a large m3 heel as in *Miohippus*, and unlike any known *Archaeohippus*. Of the upper cheek teeth, some are large and 1) mediolaterally broad as in *Miohippus*; 2) most of these have connected metalophs; 3) and fairly complete protolophs; 4) hypostyle closes postfossette. Some are smaller and less advanced with 1) metaloph not connected; 2) metaconule distinct. Cowhouse UF 40120 upper molar resembles UF 156378 RM1in several regards: 1) hypostyle almost closed; 2) metaconule not distinct.

Cowhouse Slough specimen UF 40130 lower cheek tooth is similar to lower teeth from Brooksville II: 1) broad entoconid; 2) trigonid partially enclosed lingually by wrap-around paralophid; 3) retracted cristid obliqua; 4) distinct metaconid/metastylid twinning. They are distinct in that the hypoconulid is not as pointed as in the Brooksville equids.

Cowhouse Slough equids differ from *Archaeohippus* because of the above characters and the: 1) large m3 heel; 2) very weak metastyle; 3) mediolaterally broad protocone (like *M. equinanus* and others); 4) flat metacarpal, with wide epicondyles and very long (distally projecting) keel as in some *Mesohippus* and *Miohippus*; 5) mediolaterally broad proximal phalanx III as in *Mesohippus* and *Miohippus*, but not *Archaeohippus*, *Desmatippus*, or *Parahippus*. *Archaeohippus* has rounder (cross-section) metacarpals with concave surface between scars for lateral toes. Compare against *A. mannulus*, which, though its metapodials are not as round as the metapodial of *A. blackbergi* (they are closer to *P. leonensis*), they are still much more advanced than the metapodial from Cowhouse Slough.

The Buda Local Fauna (Frailey, 1979) includes a fairly large, primitive lateral phalanx with a *Miohippus* aspect to it.

The White Springs Local Fauna (Morgan, 1989) includes *Anchippus* sp. UF 120041 partial upper molar is very large (mlw over 17 mm with ectoloph missing) with small-medium crochet, very low metaloph connection, columnar cones with space beside them. Lower dentition represented by fragments of large teeth with strong labial cingula and no cemetum.

The Franklin Phosphate Local Fauna (Simpson, 1930) has several teeth assigned to *P. leonensis*. Strong labial cingulum; no cementum; low, strongly separated metalophid; astragalus with medial condylar ridge overhanging navicular facet as in parahippines; proximal metatarsal with cuboid facet; and proximal phalanx III (UF V-3442) length/midshaft width index 28.8/15.6=1.8; this combination is not suggestive of *P. leonensis*. This equid is an advanced *Miohippus* or primitive *Desmatippus*; its low phalangeal index suggests the former.

The early to middle Hemingfordian localities of Thomas Farm (Simpson, 1932), Midway Farm (Sellards, 1916), Griscom Plantation (Colbert, 1932), Seaboard 1B (Olsen, 1964a), Colclough Hill (Olsen, 1964), and some undescribed material from the Oldsmar locality near Tampa all contain representatives of either *Archaeohippus blackbergi*, *Parahippus leonensis*, or *Anchitherium clarencei*; *Miohippus* and *Desmatippus* are absent.

Observations on Material at the AMNH

Archaeohippus sp. lower teeth from Barstow, CA AMNH 21100 is unusual. It has 1) huge hypoconulids, 2) strong metaconid-metastylid twinning, 3) wrinkled lophids, 4) big m3 heel with extra lophids. Possibly *Merychippus gunteri*.

Archaeohippus sp. cast of UCMP 37273 Flint Hill, SD has 1) pronounced groove between cristid obliqua and metastylid on relatively unworn molars. This groove is almost as deep as that seen in two teeth from Loup Fork, NB at the MCZ. Loup Fork *A. penultimus* plesiotype from MCZ has a long p4 when plotted against the Thomas Farm *A.*

blackbergi. These specimens also have cristid obliquae that are strongly separated from the metastylid, a mesohippine character. These also are probably not *Archaeohippus*.

Archaeohippus sp from New Mexico is extremely fragmentary and uninterpretable.

Voorhies (1990) identifies adult *P. cognatus* from the Norden Reservoir region of Nebraska as having very high crowned molars with lots of cementum in completely closed fossettes. Therefore, *Parahippus* includes derived species such as *P. cognatus* and *P. leonensis*, whereas *tyleri*, *nebrascensis*, *coloradensis* are all too primitive for this taxon. Adults with cement free teeth and an unconnected crochet belong in *Anchippus* (Leidy, 1868) according to Voorhhies (1990) and Albright (1998) or *Desmatippus* (MacFadden, 1998).

Parahippus sp. USNM 413002 Upper molar from B Quarry, Dawes County Nebraska, Middle of NE 1/4 sec 30, 31N, 47W Runningwater Formation, Antelope Valley has: 1) flatter ectoloph; 2) hypostyle has strong B and weak C; 3) elongate protocone; 4) lots of space in fossettes; 5) taller crown; 6) some cementum.

Parahippus sp. (*cognatus* ?) USNM 13765 R maxilla, left on exhibit as *P. cognatus*; USNM 412998 another R maxilla. Dawes Co. Nebraska, Quarry B. Coll. Ted Galusha 1934. Different from above tooth. Similar to *A. mannulus* with long P2; no crochets on P2/3, weak on P4, strong on M1-3; however, prefossette is not quite closed off by crochet. W-shaped ectoloph, metastyle not as sharp as *A. blackbergi*; Hypostyle B is weak, A and C strong. Conule on cingulum next to protocone on anterior side. Constrained space in fossettes.

FAM 7277 from Haystack Valley, John Day has mesentocuneiform facet with a vertical crest as seen in *Kalobatippus*; seen to lesser degree in F:AM 7271 paratype of *Miohippus primus* (previously *M. brachylophus*) from Haystack Valley, which also has weak MTII facets on MTIII, as in *Anchitherium*.

Mesohippus stenolophus cast of NMC 6303 has a very low and small protoconule and oblique shape overall. Very low metaloph connection; hypostyle is triangular but weakly so such that A doesn't connect with the metaloph to close postfossette lingually. NMC 6302 LM3 is similar, ectoloph not broken so weak ribs are observable; oblique shape to the tooth; hypostyle even weaker than NMC 6303; crista on ectoloph not quite in contact with metaloph; metastyle is weak and low. Protocone extends too far labially to be *Archaeohippus*.

Type of *Parahippus pristinus* has a large malar fossa. However, this structure appears to be an artifact of preparation. Much of the external surface of the skull is absent. The bone inside the malar fossa may be an internal bone layer in a sinus. *P. pristinus* has 1) premaxilla with strongly curving incisor roots, flat wear on crowns; 2) very thin bone that may have contributed to the probable over-preparation that created the deep malar fossa; 3) extremely long metapodials; 4) large, primitive facets on the proximal metapodials; 5) round head on metapodials (like *Archaeohippus*). It is the untested opinion of the present author that *P. pawniensis*, *P. atavus* (sometimes called *P. pawniensis atavus*) and *P. pristinus* are all very closely related to each other, and may represent chronoclinal forms of one species. *P. atavus* at the AMNH has metacarpal ~125 mm long, somewhat larger than *Archaeohippus* and very similar in morphology.

Lusk WY Early Arikareean Gering Fm; magnum has 1) large, projecting facet for articulation with lunatum; 2) distal metapodials have large keel, thick and long, though it doesn't extend anterior except as a low hump; 3) large unciform facet as in another Lusk specimen, although not as large as *Desmatippus* or *Hypohippus*; 4) lateral metapodials apl deep but not overly thick in mlw; 5) crania with well-developed lacrimal fossa; 6) very thin preorbital border; 7) some pocketing of fossa: 8) orbit is over anterior M2 like early *Archaeohippus*. Some of this material was previously assigned to *P. pristinus*.

Lusk horse (found north of Lusk in 1931) broadly resembles *Archaeohippus*, but the protocone is too broad and extends too far labially toward the paracone. A Lusk skull has 1) connected metalophs; 2) slightly larger size than *Archaeohippus blackbergi*; 3) very plump protocone and hypocone (unlike *Archaeohippus*); 4) weak metastyle; 5) shallow DPOF without pocketing; 6) robust side toes; 7) oblique proximal articulation of the third metapodial, not rounded with almost centrally placed volar facet and tubercle platform as in *Archaeohippus*; 8) very large unciform facet (twice the size of *Archaeohippus*).

Turtle Butte *Archaeohippus* sp. does not strongly resemble *Archaeohippus*, although the astragulus has a groove that partially separates the posteromesial calcaneal facet from the navicular facet that is seen also in *Archaeohippus*, *Parahippus*, and *M. equinanus*. Differs from *Archaeohippus* in these regards: 1) m3 is large and complex as in *Miohippus*; 2) no metastylid; 3) metalophid is strongly retracted from the metaconid; 4) short, wide proximal phalanx III.

Desmatippus F:AM 71592 Barstovian Colorado has 1) MC III with large volar tubercle (not seen in *Hypohippus*); 2) very large unciform facet that wraps around the top of the MCIV (seen also in *Hypohippus*); 3) side toes robust in ml plane, not too thick in ap; 4) teeth low-crowned with small crochets; 5) big lacrimal fossa with pocket, no malar fossa 6) crease between nasals as in *Hypohippus giganteus*, frontals only slightly depressed; 7) tooth replacement p2-4 simultaneous, slightly preceded by m1-2 as in *Archaeohippus*; 8) M3 reduction in *Hypohippus* and *Desmatippus* is not as in *Archaeohippus*. The tooth is small and square without loss of the hypocone (which causes the M3 to be triangular in *A. blackbergi*).

Hypohippus has: 1) uppers that not only lack ribs, they often have clefts or creases instead; 2) some identified as *H. wardi* from Olcott Formation in Texas have m3 heel so reduced it resembles hypoconulid from other cheek teeth; 3) *H. giganteus* from Clarendonian Ash Hollow Formation in Nebraska lives up to its name, and has a deep fossa that goes low in malar (as in *Archaeohippus*) but with a very wide preorbital border (as in all *Hypohippus*, and unlike *Archaeohippus*); 4) deep depression in frontals that extends down nasals; 5) nasal notch retracted to P2.

Megahippus matthewi F:AM 60700 from the Clarendonian Valentine Formation of Nebraska has 1) large facial fossa like *Hypohippus*; 2) large sagittal crest; 3) depressed frontals as in *H. giganteus*.

Kalabatippus praestans type has 1) teeth like *Hypohippus*; 2) nasal and frontal depression; 3) shallow fossa; 4) thin preorbital border as in *Archaeohippus* and *Desmatippus*.

Taxa with very primitive feet include *Hypohippus*, *Megahippus*, *Anchitherium*, *Kalabatippus*, and those specimens assigned from the Barstovian of Colorado to

Desmatippus that have robust side toes, large unciform facet (and no malar fossa in skull).

Comments on Materials at USNM

USNM 475915 Borrow Pit on E of US 13, 5.2 miles S of Smyrna 0.7 miles S of Lake Garrison, Kent County Delaware. Cast of *Archaeohippus* sp. has big, plate-like, fully enclosed hypostylid as seen in *A. mannulus*. AP length=10.7mm, ML anterior length=7.4 mm, ML posterior length=8.5 mm. Good twinning of metaconid/metastylid, though no sign of a crease on the side at this stage of wear. In early wear, cristid is still distinct from metastylid, but not retracted. USNM 475781 has little wear. Hypostylid is more columnar, but thick and fully enameled. AP length=10mm, ML anterior length=6.6 mm, ML posterior length=6 mm.

USNM 25142 *Archaeohippus* cf. *minimus*, portion of right maxilla with P3-M3. Lower Madison Mountains, southern Montana, Madison Valley, Barstovian. Collected by Sternberg 1931. Looks like *A. blackbergi* with small crochets on P34, but larger than *A. blackbergi*.

Uncatalogued material from Upper Willow Creek, Baker County, Oregon collected 9/10/1880 by J. Warfield includes one *Archaeohippus* astragulus, one *Parahippus* astragulus, two *Parahippus* proximal phalanx III, and one *Anchitherium* medial phalanx III. Therefore, the Thomas Farm equid fauna was pan-continental.

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BIOGRAPHICAL SKETCH

Jay Alfred O'Sullivan was born May 27, 1965, at Paterson General Hospital when it was still in Paterson, New Jersey. He spent his first 21 years in Hawthorne, New Jersey. Born the fourth of five children, Jay learned early on the wisdom of compromise and the necessity of being a good listener. Early in Jay's life, his father, Joseph O'Sullivan, and mother, Joan Marie Kuiper O'Sullivan, instilled in him an abiding love for, and respect of, nature and science. Day trips for hikes, fishing, mineral collecting, or simple observation of wild rats along the Passaic River, combined with a steady flow of PBS programming to create an elegant family philosophy: the Universe is old, large, complicated, and beautiful, and we are part of it. As a result, Jay spent significant portions of his childhood ankle deep in Goffle Brook harassing crayfish and salamanders.

Jay attended Theodore Roosevelt Elementary School, then Hawthorne High School, which he left midway through his senior year to attend The William Paterson College (now University) of Wayne, New Jersey. This same sequence had characterized the early educational careers of siblings Joseph William, Judy Lynn, and Jeffrey Stephen O'Sullivan. Only younger sister Jennifer Lee O'Sullivan deviated from this path by never attending ol' "Bill on the Hill." Upon leaving high school, Jay planned on becoming a vertebrate paleontologist. Somehow, he found himself studying anthropology and sociology at William Paterson. After two-and-a-half years, Jay took a year off, then transferred to Arizona State University in Tempe, Arizona, with two friends and fellow punk musicians. At ASU, Jay explored both archaeology and primate behavior. He also met Kym Sewall Grigsby, who would leave ASU with Jay for New York City.

In New York, while Kym finished her degree in English at New York University, Jay started his master's in anthropology at Hunter College, City University of New York. The M.A. program at Hunter was designed for working students; all the courses were offered at night. Also, it afforded students the luxury of not knowing what subdiscipline of anthropology they wanted to pursue until completing the first year. This was an ideal situation for Jay, who had entered the program believing he wanted to become a cultural anthropologist. A classmate told him to avoid a course in functional morphology taught by vertebrate paleontologist Frederick S. Szalay, so Jay signed up for the class. During that challenging semester, he was reminded what he had wanted to do with his life since childhood, the career choice he had put in his high school yearbook entry. Jay asked Fred to be his advisor and to give him a project that would demonstrate his desire to work outside the order Primates; thus was born the opossum thesis.

Also during this period was born Sylvan Patrick O'Sullivan, the beautiful son of Kym and Jay, and Jay's initial incentive to pursue a Ph.D. and a career in academia. With an almost two-year-old Sylvan in tow, the O'Sullivans moved to Gainesville, Florida, where Jay had been accepted to study with Bruce J. MacFadden in the Department of Zoology, University of Florida. It was here that not only this dissertation, but two more beautiful children, Joanna William O'Sullivan and Quinn Jeremiah O'Sullivan, were born.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Bruce J MacFadden

Bruce J. MacFadden, Chairman
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Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Richard C. Hulbert

Richard C. Hulbert
Coordinator of Museum Operations
Florida Museum of Natural History

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Douglas S. Jones

Douglas S. Jones
Professor of Geology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Brian K. McNab
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

S. David Webb

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 2002

Dean, Graduate School